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VOLUME XII MARCH, 1920 No. 2

INTESTINAL HELMINTHS IN INDIANS IN MESOPOTAMIA.

BY CHARLES L. BOULENGER, M.A., D.Sc.

(Reader in Helminthology, University of Birmingham.)

WHILST engaged on protozoological investigations of dysentery and allied diseases in Mesopotamia I had the opportunity of examining the stools of a large number of hospital patients, both British and Indian, and of noting the presence of worm ova as well as protozoan parasites.

The British patients proved to be almost entirely free from helminth infection; on the other hand, as was to be expected, such parasites were of frequent occurrence in the Indians and the object of this note is to give a brief account of the incidence of the different forms met with.

The stool examinations were made primarily for protozoan parasites, the samples were not sedimented or centrifuged and at the most two smears were examined for each case. According to Clayton Lane (1916), to establish the absence of worm infection at least fifteen smears must be examined from each faecal sample; it is obvious therefore that the percentages obtained by me for the different worms are too low, probably about half those which would have been found had the proper helminthological technique been employed. The figures are however, in my opinion, worth publication, since very few data of this kind are available, moreover they afford me an opportunity of calling particular attention to certain worms observed.

The total number of individuals examined was 1180, these consisted chiefly of dysentery cases and patients convalescent from that disease, a number suffering from other complaints (*e.g.* anaemia) are however included, as well as 200 healthy men, selected as "controls" in various investigations.

The findings are shown in the following table:

Number of individuals examined	1180	
Taenia saginata	14 = 1·2	%
Hymenolepis nana	23 = 2	,,
Ascaris lumbricoides	62 = 5·2	,,
Oxyuris vermicularis	1 = 0·08	,,
Agchylostoma duodenale / *Necator americanus*	219 = 18·5	,,
Trichostrongylus sp.	14 = 1·2	,,
Strongyloides stercoralis	6 = 0·5	,,
Trichuris trichiurus	59 = 5	,,

The percentages for some of the commoner parasites, *e.g. Ascaris lumbricoides*, seem very low; this is due, partly, as explained above, to the technique employed and partly, no doubt, to the fact that the majority of the individuals examined were hospital patients who had already undergone some form of treatment. Even after allowance is made for these factors the infections are not heavy as compared with those of natives examined in India (cf. Clayton Lane, 1916); a similar series of Turkish prisoners of war examined by precisely the same methods gave me a percentage of 22·2 for *Ascaris*, *i.e.* more than four times that in Indians in Mesopotamia.

The two hookworms are considered together, since the eggs of *Agchylostoma* and *Necator* are difficult to distinguish with any certainty unless large series of measurements are made, both worms were however frequently recovered after the administration of vermifuges. *Necator* seemed rather more common than *Agchylostoma* and my records of the egg measurements show the relative abundance of the two forms to be as 4: 3.

The eggs identified as those of *Trichostrongylus* measured 80–99 microns in length and when passed in the faeces were in a late "morula" stage, *i.e.* in a much later stage of development than those of the hookworms; they resembled in every respect the eggs of species of *Trichostrongylus* with which I was familiar in domestic animals. The extreme measurements of the ova are slightly in excess of those given by various authors for the different species of this genus, the latter measurements are however seemingly based on eggs taken from the uteri. I have frequently noted in various Strongyles that measurements of ova from faeces are often greater than those of ova taken from the maternal tissues.

The parent worms were unfortunately never recovered after the administration of vermifuges, in spite of several attempts.

Trichostrongylus ova were also frequently observed in the faeces of Kurdish and Persian coolies employed in various labour corps in Mesopotamia.

Until recently three species of *Trichostrongylus* (*T. colubriformis*, *T. vitrinus* and *T. probolurus*) had been recorded by Looss (1905) as occasional parasites of man in Egypt; in 1914, however, Jimbo described a fourth species, *T. orientalis*, found in a large percentage of cadavers examined by him in Japan; as suggested by Ransom (1916) the various species of this genus are probably much commoner parasites of man than is generally supposed and their distribution in man will no doubt be greatly extended as increased emphasis is laid upon laboratory methods in medical diagnosis.

Hymenolepis nana is another parasite to which I desire to call particular attention. As shown in the table, it was the commonest Tapeworm met with in Indians. The occurrence of this species is, I understand, well known to many medical men working in India, it is a fact however which for some reason or other has not found its way into the text-books on Parasitology and Tropical Medicine; even in the more recent editions and the newer works (*e.g.* Fantham, Stephens and Theobald, 1916) the distribution of this parasite

is constantly given as: parts of Europe, N. and S. America, Egypt, Siam, Japan, and the Philippines.

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ON SOME NEMATODE PARASITES OF THE ZEBRA.

By CHARLES L. BOULENGER, M.A., D.Sc.

(*Reader in Helminthology, University of Birmingham.*)

(With 7 Text-figures.)

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INTRODUCTION.

Having during the last few years been particularly interested in the Nematode parasites of horses and donkeys I was very pleased to find a tube containing Strongyles from the zebra among some material recently forwarded to me by Professor G. H. F. Nuttall, F.R.S. These worms formed part of a collection of Helminths from Nairobi, British East Africa, which had been sent for identification by Mr R. Eustace Montgomery, Director of the Nairobi Veterinary Pathological Laboratory.

The specimens were in a good state of preservation and, although not numerous, they included representatives of eight species, three hitherto undescribed, one of which is taken as the type of a new genus. The specific identity of the host was unfortunately not ascertained, the worms being labelled "Zebra, R. Ruaraka."

As pointed out by Leiper (1911), the Nematodes parasitic in the zebra consist of a number of species occurring in the domestic equines as well as others peculiar to itself, of the latter among the bursate forms perhaps the most interesting are those included by that authority in the genus *Cylindropharynx*. Both the known species of this genus are to be found in Mr Montgomery's collection, and, whilst describing some new forms of *Cylicostominae* in this paper, I take the opportunity of somewhat amplifying Leiper's descriptions of these species.

The worms from the Nairobi material have been identified as follows:

1. *Strongylus vulgaris* (Looss, 1900).
2. *Cylindropharynx brevicauda* Leiper, 1911.
3. „ *longicauda* Leiper, 1911.

4. *Cylicostomum minutum* Yorke and Macfie, 1918.
5. ,, *zebrae* sp. n.
6. ,, *Montgomeryi* sp. n.
7. *Triodontophorus serratus* (Looss, 1900).
8. *Craterostomum tenuicauda* gen. et sp. nn.

The species numbered 1, 4 and 7 are also parasites of the domestic equines.

Family STRONGYLIDAE.

Subfamily CYLICOSTOMINAE Railliet, 1914.

Genus CYLINDROPHARYNX Leiper, 1911.

Cylindropharynx brevicauda Leiper, 1911.

The type species of the genus is more abundantly represented in Mr Montgomery's collection than *C. longicauda*. Leiper has given a fairly complete account of the species, a few characters are, however, omitted from his description and I take this opportunity of adding to our knowledge of certain important structures, *e.g.* the oral leaf-crowns and the external genitalia in the male sex.

The specimens before me measure: Females, 5·6–8 mm., males, 5–7·3 mm. in length; maximum breadth of the body, about 0·45 mm.

The head (measured at the anterior extremity of the mouth-capsule) has a diameter of 0·12–0·15 mm. The mouth is circular and surrounded by a mouth-collar which appears almost semicircular in a lateral view (Text-fig. 1).

The lateral papillae are not prominent, they are situated in a slight depression of the oral margin and have trifurcated extremities, recalling the similar structures in *Oesophagodontus robustus* (cf. Boulenger, 1916). The submedian papillae are conspicuous, each consists of a leaf-shaped appendage carried on a cylindrical base (Text-fig. 1, A).

The anterior leaf-crown consists of six triangular elements unequal in size and arranged in a very characteristic manner; four occupy a submedian position and are of equal, relatively small size, the two remaining leaves are much broader and situated laterally, each is usually notched at the apex and longitudinally grooved, suggesting an origin by fusion of at least two elements. Owing to the lack of radial symmetry of these organs, the head presents very different appearances when viewed laterally or from the dorsal or ventral sides (Text-fig. 1, A and B).

The posterior leaf-crown consists of a circle of twelve broad, elongated leaves arising from the anterior margin of the mouth-capsule, the leaves are extremely thick, in profile (Text-fig. 1, A) they might be taken for anteriorly directed branches of the oral capsule.

The very characteristic mouth-capsule measures 0·3–0·4 mm. in length with a maximum diameter of 0·09–0·12 mm., its internal surface is lined with a transparent chitinous layer, as in many species of *Cylicostomum*.

A small oesophageal funnel occupies the anterior cavity of the oesophagus, the latter being almost cylindrical in shape and measuring 0·47–0·53 mm. in length with a breadth of 0·13–0·17 mm.

Cervical papillae are situated 0·45 mm. from the anterior extremity.

Female. The tail is pointed; the vulva is situated 0·45–0·75 mm., the anus 0·15–0·2 mm. from the posterior extremity, the different measurements being due to the various degrees of contraction of the caudal region.

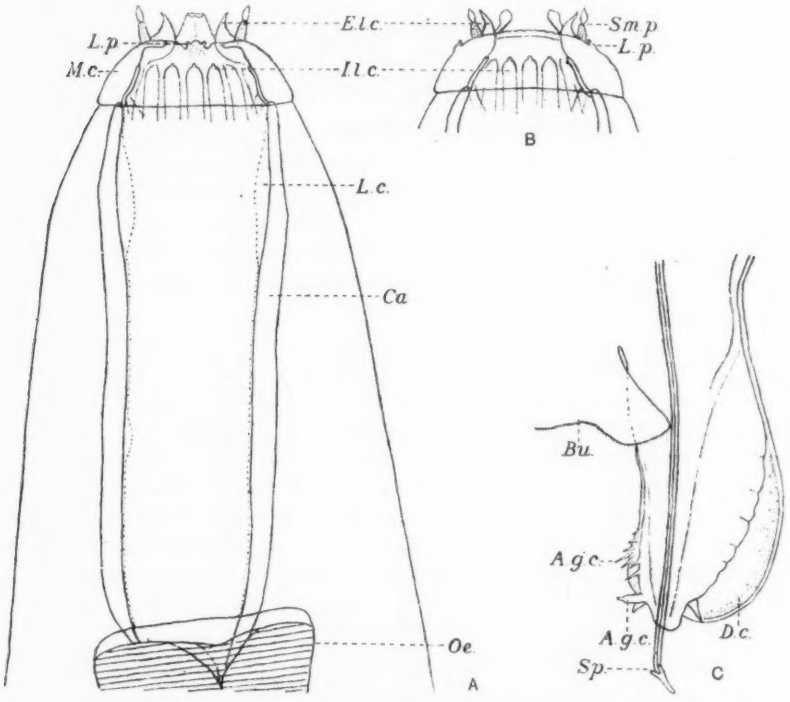

Fig. 1. *Cylindropharynx brevicauda* Leiper. A. Anterior extremity in lateral view. B. Anterior extremity, dorsal view × 215. C. Genital cone and adjacent structures in the male, × about 125.

Male. As described by Leiper, the males of this species are characterised by the large genital cone, the latter is almost cylindrical (up to 0·4 mm. in length with a breadth of 0·17 mm.) and completely surrounded by the dermal collar which, however, shows its greatest development on the ventral surface (Text-fig. 1, c).

The appendages of the genital cone are quite peculiar, a pair of finger-shaped appendages with rounded ends occur just behind the genital opening, whilst an irregular number of delicate pointed processes are scattered over the dorsal surface of the cone (Text-fig. 1, c).

As in *Triodontophorus* the bursa has a denticulated margin, the dorsal lobe measures about 0·2 mm. in length, the lateral lobes are narrower than those of *C. longicauda* and do not completely embrace the genital cone. The external branch of the posterior ray is deeply bifurcated (Text-fig. 2, C).

The spicules are long (about 1·1 mm.) and rather stout, they have hook-like terminations recalling those of *Triodontophorus*.

Cylindropharynx longicauda Leiper, 1911.

Four specimens of this species occur in the Nairobi material, two males and two females, the former measuring 4·7 and 5·8 mm. in length, the latter 6·2 and 7 mm. respectively. The greatest breadth of the body is about 0·45 mm.

The head has a breadth of 0·14–0·15 mm. The mouth-collar and the leaf-crowns resemble those of the type species.

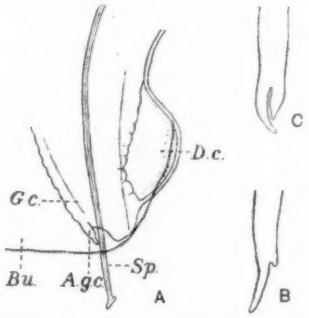

Fig. 2. *Cylindropharynx longicauda* Leiper. A. Genital cone of the male. B. External branch of the dorsal ray. C. *C. brevicauda*, external branch of the dorsal ray, × about 125.

The mouth-capsule is smaller and considerably shorter than that of *C. brevicauda*, measuring 0·18–0·2 mm. in length, with a breadth of 0·07–0·09 mm.

The oesophagus is almost as long as in the type species (0·42–0·45 mm.), but much more slender, the greatest breadth being 0·08–0·1 mm.

Female. In the specimens before me the vulva opens 1·1 and 1·2 mm., the anus 0·28 mm. from the posterior extremity. The tail is long and pointed.

Male. The bursa is broader than in *C. brevicauda*, measuring nearly 0·5 mm. in a lateral view. The lateral lobes enclose the genital cone which is shorter and more globular (Text-fig. 2, A) than in that species. Leiper describes the external branch of the posterior ray as undivided, in the Nairobi specimens a small branch is given off close to the termination of the ray in the same position as the much longer branch of *C. brevicauda* (Text-fig. 2, B).

The appendages of the genital cone consist of a single pair of rather stout, finger-shaped processes.

The spicules are shorter (0·78 mm.) and more slender than those of the type species and are provided with less powerful terminal hooks.

As pointed out by Leiper, the species closely resembles *C. brevicauda*, the chief points of difference being: the smaller mouth-capsule, the more slender oesophagus, the elongated caudal region of the female and the structure of the bursa and the genital cone in the male.

Genus Cylicostomum Railliet and Henry, 1902.

Cylicostomum zebrae sp. n.

Specific Diagnosis. *Cylicostomum.* A fairly large, robust species represented in the collection by three specimens, only two of which are adults, one female and one male, measuring 9·8 and 8·5 mm. in length respectively. The maximum thickness in both sexes is about 0·8 mm. Both worms have con-

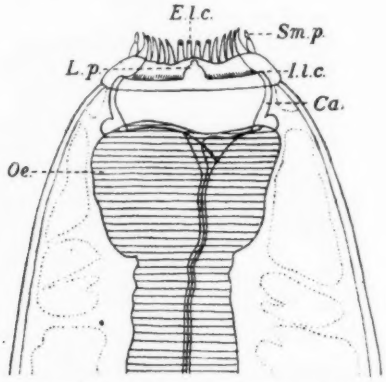

Fig. 3. *Cylicostomum zebrae* sp. n. Anterior extremity in lateral view, × about 125.

siderably shrunk during fixation as is shown by the ratio of length to breadth, during life they must have been considerably more elongated than the figures show. The head is broad (0·27–0·3 mm.), not separated from the body by a neck constriction. The mouth collar is relatively low and depressed at the margins except in the neighbourhood of the lateral papillae. The latter are large and very prominent, forming a conspicuous feature in a dorsal or ventral view of the head (Text-fig. 4).

The submedian head papillae are long, with leaf-shaped terminal appendages.

The mouth is oval in shape, the longer axis being directed dorso-ventrally. The external leaf-crown consists of about 32 pointed leaves, the elements of the internal leaf-crown are very inconspicuous and very small, appearing as a ring of fine striae immediately in front of the mouth-capsule (Text-fig. 3).

The mouth capsule is short measuring 0·07 mm. in length, with a breadth of 0·2 mm., its walls are thin except in the posterior region where they are

greatly thickened to form a "hoop-like" ring similar to that described by Looss (1901) in *C. elongatum* and *C. auriculatum*. There is no dorsal gutter.

The oesophageal funnel is very large and enclosed in the broad anterior end of the oesophagus, the latter, 0·75–0·85 mm. in length, is 0·2–0·25 mm. wide in the region of the funnel, narrowing to 0·12 mm. at the level of the nerve-ring and broadening out again to 0·23–0·25 mm. in the terminal region (Text-fig. 4).

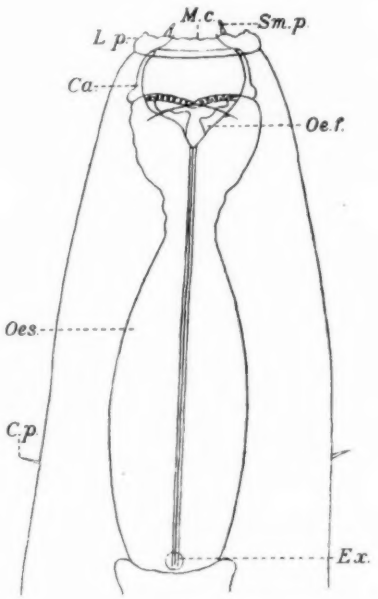

Fig. 4. *Cylicostomum zebrae* sp. n. Ventral view of the anterior extremity, × about 75.

The chitinous lining of the oesophageal funnel is highly developed forming tooth-like ridges, but owing to the thickness of the oesophagus in this region their exact arrangement could not be ascertained, they are, however, indicated in Text-fig. 4.

The excretory pore opens at the level of the junction of oesophagus and intestine. The cervical papillae are a little further forward, 0·8 mm. from the anterior extremity of the body.

Female. The vulva is 0·25 mm. from the posterior extremity, at this level the body has a thickness of 0·23 mm. The anus is 0·1 mm. behind the vulva. Posterior to the anus the depth of the body decreases suddenly, forming a flat triangular tail. The vagina has a length of about 0·5 mm.

Male. The bursa (Text-fig. 5) is very similar to that of *C. insigne* Boulenger; the dorsal lobe is large and broad. The dermal collar is well developed

and surrounds the genital cone. The appendages of the genital cone are in the form of broad oval plates, fused together in the middle line.

This form evidently belongs to the group of species which includes *C. auriculatum* Looss, *C. elongatum* Looss and *C. insigne* Boulenger, agreeing with these in the general formation of the head and in the structure of the male bursa and its appendages. Apart from minor characters it differs from these species in the shape of the oesophagus with its enlarged anterior extremity and the greater development of the oesophageal funnel.

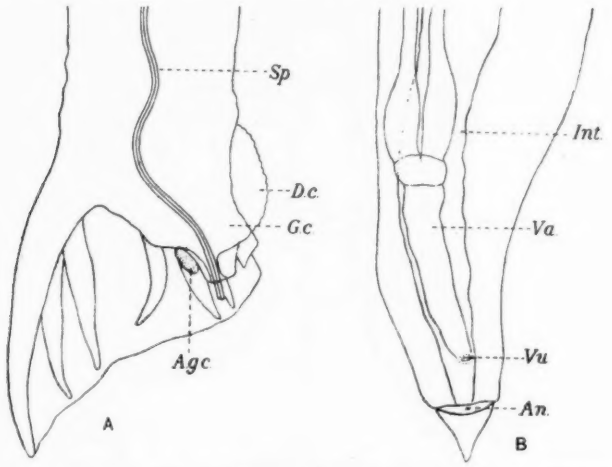

Fig. 5. *Cylicostomum zebrae* sp. n. A. Bursa of male from right side. B. Posterior extremity of female, ventral view, × about 75.

Cylicostomum Montgomeryi sp. n.

Specific Diagnosis. *Cylicostomum.* A small species, females 4·5–6·5 mm., males 4·3–6 mm. in length. The greatest thickness of the body is 0·28 mm., decreasing to 0·2 mm. at the level of the commencement of the intestine.

The head is 0·08–0·09 mm. broad, not separated from the body by a constriction to form a neck.

The mouth is oval, the dorso-ventral axis being a little shorter than the lateral. The mouth collar is thick and depressed at the margins (Text-fig. 6).

The lateral papillae are prominent, the submedian slender with leaf-shaped appendages.

The anterior leaf-crown consists of about 18 slender, pointed leaves, the posterior leaf-crown of twice that number of rather similar but shorter elements (Text-fig. 6).

The mouth-capsule is characterised by its peculiar bilateral symmetry, its dorsal and ventral walls being considerably higher (0·032 mm.) than the lateral walls (0·022 mm.); this absence of radial symmetry makes an optical

section of the head in a lateral view present a totally different appearance to that viewed dorso-ventrally (Text-fig. 6, A and B).

There is no dorsal gutter. The oesophageal funnel is poorly developed.

The oesophagus is slender with an average length of 0·33 mm. Cervical papillae are present at the same level as the excretory pore, 0·24 mm. from the anterior extremity.

Female. The vulva is 0·13 mm., the anus 0·06 mm. from the posterior extremity of the body. The tail region behind the anus is narrow and ends in a fine point.

Male. The bursa is 0·25 mm. broad when viewed from the dorsal or ventral surface, the dorsal lobe is of medium length (0·12 mm.). The dermal collar is poorly developed and almost flat on the ventral surface of the genital cone. The latter is short, its appendages are similar to those of *C. tetracanthum* (Mehlis), *i.e.* ovoid in shape with a short blunt point on the posterior margin.

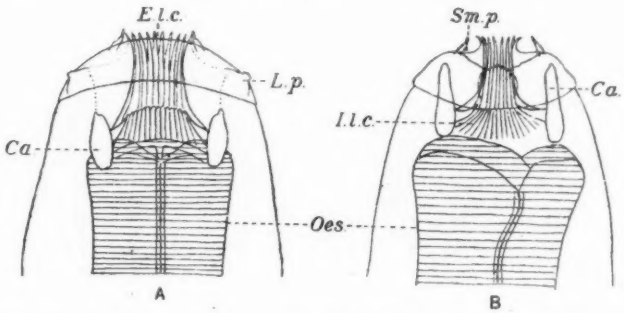

Fig. 6. *Cylicostomum Montgomeryi* sp. n. Anterior extremity. A. Dorsal view. B. Lateral view, × about 350.

In the structure of its mouth capsule this form differs from all other known species of *Cylicostomum* with the exception of *C. falciferum* (Cobbold, 1882), a parasite of the Elephant now placed in a separate genus *Murshidia* Lane, 1914. In the latter species, however, the bilateral symmetry extends to the elements of the leaf-crown; this is not the case in *C. Montgomeryi*, where these structures are radially arranged.

Genus CRATEROSTOMUM gen. n.

Type species: *C. tenuicauda* sp. n. Closely allied to *Triodontophorus* Looss, differing from this genus by the absence of teeth projecting into the mouth-capsule.

Craterostomum tenuicauda sp. n.

Small, rather robust worms; the type specimens consist of three females only, 4–5·5 mm. in length. The cuticle of the body is transversely ringed. Body with a maximum breadth of nearly 0·4 mm., reduced to 0·28–0·32 mm. at the level of the termination of the oesophagus.

The head is 0·17 mm. broad, not separated from the body by a constriction.

The mouth is very small and circular, the mouth-collar narrow and depressed at the margins (Text-fig. 7, A).

The lateral papillae are not prominent, the submedian papillae small with leaf-shaped terminations.

The external leaf-crown consists of nine comparatively large almost triangular leaves arising from the inside of the mouth-collar as in *Triodontophorus* spp. The elements of the internal leaf-crown are also similar to those found in that genus, being septa-like projections, numbering 18 only.

The mouth-capsule and dorsal gutter (Text-fig. 7, A) are also similar in structure to those of *Triodontophorus*, the former is a little broader than long, measuring 0·07 × 0·05 mm.

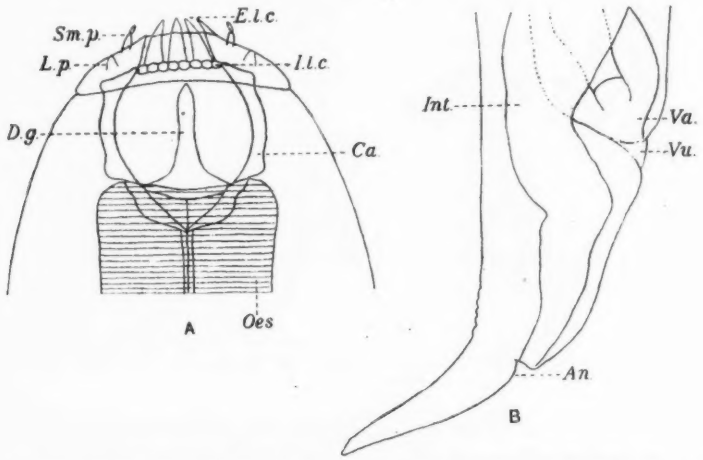

Fig. 7. *Craterostomum tenuicauda* gen. et sp. nn. A. Anterior extremity, ventral view, × about 350. B. Posterior extremity of female, lateral view, × about 125.

The oesophageal funnel is poorly developed and there are no teeth projecting from it into the mouth-capsule. The funnel is similar to that found in many species of *Cylicostomum*.

The oesophagus is narrow and has a length of 0·37–0·4 mm. Excretory pore and cervical papillae are at the same level, about 0·25 mm. from the anterior extremity.

The female genitalia are similar to those of some species of *Triodontophorus*. The vagina is very short (Text-fig. 7, B). The vulva opens 0·53–0·57 mm. from the posterior extremity; at this level the body has a thickness of 0·2 mm., this is reduced to 0·07–0·08 mm. in the anal region, 0·25–0·27 mm. from the end of the body. The tail region behind the anus is much attenuated (Text-fig. 7, B) and terminates in a point.

Although vagina and uteri are well developed in all the specimens, these as yet contain no mature ova.

In the majority of its characters this species very closely resembles certain species of *Triodontophorus*, and is only excluded from that genus on account of the absence of teeth in the mouth-capsule. The mouth is relatively smaller and the number of elements of the leaf-crowns considerably less than in any known species of *Triodontophorus*.

On account of the small size of the type-specimens and the absence of ripe ova, these worms might be considered as young stages of some species of *Triodontophorus*. This seems to me highly improbable, the specimens before me have evidently undergone the final moult and are obviously almost fully developed even if they have not reached their complete size. Species of *Triodontophorus* at this stage have the capsule-teeth fully developed, I have seen these structures in specimens smaller than those described above.

The absence of these teeth therefore makes it impossible to include the worms in the genus *Triodontophorus* in spite of their close affinity; I have therefore been obliged to regard them as the types of a new genus.

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EXPLANATION OF LETTERING IN TEXT-FIGURES 1–7.

A.g.c. Appendage of the genital cone.
An. Anus.
Bu. Margin of the bursa.
Ca. Wall of mouth-capsule.
C.p. Cervical papillae.
D.c. Dermal collar of genital cone.
D.g. Dorsal gutter.
E.l.c. External leaf-crown.
Ex. Excretory pore.
G.c. Genital cone.
I.l.c. Internal leaf-crown.
Int. Intestine.
L.p. Lateral papilla.
M.c. Mouth collar.
Oes. Oesophagus.
Oe.f. Oesophageal funnel.
Sm.p. Submedian papilla.
Sp. Spicule.
Va. Vagina.
Vu. Vulva.

A PARASITIC SPIRAL ORGANISM IN THE STOMACH OF THE CAT.

By R. K. S. LIM.

(*From the Department of Physiology, University of Edinburgh.*)

(With Plate VII).

While examining sections of the apparently normal cat's stomach, clusters of organisms were found within the lumina of numerous ducts and glands—especially of the pyloric region. Further examination, employing various methods of staining, revealed the spiral nature of the organisms. The presence of large numbers suggested that they were actively growing and in the absence of obvious gastric disturbance in the cats in which they were found, it was concluded that they were non-pathogenic parasites.

The author has been unable to find any reference in bacteriological literature to such an organism in the cat, although Noguchi (1915–16) refers to the finding by Bell and Ruquet of a similar form of organism in the stomach of the dog. Spiral organisms have also been described by Lucet (1910) in a case of gastro-enteritis in the dog.

DISTRIBUTION.

Eight animals were affected: they had all been in the laboratory for some months. Cats which were killed immediately on admission or which had been isolated, were unaffected. Rabbits which had been kept in adjacent cages were not infected.

The stomach was the only organ in which the organisms (hereinafter referred to as "spirochaetes") were found, except a few in the duodenum, close to the pyloric sphincter. Preparations from the liver, spleen and bone marrow were negative. Within the stomach, the spirochaetes were found throughout the whole fundus, including the cardia, and in the pyloric antrum and canal. They were most numerous in the latter situation. It should be noted that in the cat, oxyntic cells are only absent within a narrow area, half to three-quarters of an inch, proximal to the pyloric sphincter, and that therefore the fundus and the major portion of the antrum are histologically, and probably functionally, similar. The term "fundus" in the following description is applied to the whole area of the stomach bearing oxyntic cells, and "pylorus" to the narrow area devoid of them.

In the fundus region, groups of spirochaetes may usually be seen within the lumen of the tubules in the middle zone of the mucosa, where the oxyntic cells occur most abundantly and where they frequently abut directly on the lumen. In sections stained with alcoholic eosin and methylene blue (*vide* Lim, 1919) and in those stained with polychrome methylene blue alone, spirochaetes can be shown within the oxyntic cells[1], lying either in large clear spaces, enclosed by a membrane or amongst the granules in the interior of the cells (see Plate VII, figs. 2 and 3). Deeper down in the mucosa, where there are few oxyntic cells, only isolated organisms are present. They are not seen in the interior of the central or peptic cells.

In the pylorus proper, dense masses of spirochaetes occur at all levels of the mucosa, but only within the lumina of the ducts and secretory tubules (Plate VII, fig. 1), which are extremely wide in this region. No spirochaetes are visible outside the glands, either in the mucous, submucous or muscular layers.

The presence of organisms does not alter the histological appearance of the stomach further than has been described above.

MORPHOLOGY.

Measurements. The spirochaetes have been found to average in length from 4 to 8μ in preparations taken direct from the fresh stomach and examined immediately. In stained films, somewhat longer forms are sometimes met with. The breadth varies from 0·75 to 1μ and the thickness of the spiral, which is cylindrical, from 0·25 to 0·5μ. Some of the smaller spirochaetes are extremely slender and have a spiral thickness of less than 0·2μ. The spirals are regular, and closely set together, there being usually about 7 to 8 spirals in each spirochaete of from 5 to 6μ. Occasionally as many as 14 spirals may be present, especially in the large forms. The spirochaetes are generally straight, but may exhibit one or more waves or curves (see Figs. 1, 3 and 5). Both extremities are tapered. When compared with the organism found in the dog[2] (Pl. VII, fig. 4), the cat spirochaete appears to be nearly of the same size (perhaps a little shorter), but differs in having more numerous and more regular spirals.

Reaction to stains. The spirochaetes stain slightly with Gram, *i.e.* they are not perfectly alcohol-fast. They are readily stained by most aniline dyes, especially when any of the Romanowsky combinations are used. With Giemsa, they appear bluish, with alcoholic eosin and methylene blue, blue, and with polychrome methylene blue, violet or purple. For clearness of staining, polychrome methylene blue is undoubtedly the best, both for smears and sections; it should be applied for 2 to 3 minutes. The Levaditi method has given poor results in the author's hands. Stained specimens of

[1] I have received an unpublished diagram from Dr Murray, drawn in 1907, showing spirochaetes within the oxyntic cells of the dog's stomach.

[2] I am indebted to Prof. Ashworth for a smear preparation (and a drawing) made by Dr J. Murray in 1907, from which the above comparison was made and a photograph taken.

the spirochaetes often exhibit granules and vacuoles. The granules stain darkly with the basic dye and are undoubtedly chromidia; they are inconstant in number (see Pl. VII, fig. 5). Vacuoles are not nearly so common, and may be artefacts resulting from overheating. Very broad forms of the spirochaete are probably also due to this cause.

Behaviour of living spirochaetes. If a little of the gastric mucosa is scraped off and transferred to a slide, the spirochaetes may be easily studied without the use of the dark ground illumination. They are highly refractile and quickly catch the eye, by the distinctness and regularity of their spirals. One or two more highly refractile spots may be seen at one or both ends of some of the organisms, but, otherwise, they appear homogeneous and structureless. When not in progression, the spirochaetes are seen in various attitudes, either straight, curved like a semicircle, or more completely, like a loop, and show one or other of the following movements which may be very active:

(1) An intermittent corkscrew-like motion of their spirals, sometimes in one direction, and sometimes in the reverse direction. Occasionally, one end appears to turn more slowly than the other. (2) Large spiral movements, superadded to the smaller movements. (3) A circular sweeping movement of one extremity. (4) Lateral oscillation of the whole organism. (5) A rotary disturbance of the fluid medium at one end of the organism, although the visible extremity of the spirochaete is not in motion. This seems to suggest the presence of a fine terminal filament (flagellum).

The behaviour of some spirochaetes in the proximity of cells is interesting. They ram the cell and spiral or corkscrew furiously, occasionally giving large circular sweeps with their free ends. Suddenly they disengage themselves, turn a "somersault" and repeat the performance with the former free end. No spirochaetes, however, have been actually observed to penetrate a cell by this means. The method of progression is difficult to analyse, but it appears to consist of a combination of corkscrew and lateral movements.

CULTIVATION.

All attempts at cultivation have hitherto failed. Deep agar, cooked-meat, and gastric digests, with or without pepsin, HCl or serum, have been used with no success. Partial anaerobiosis was maintained in all cases, except when agar was employed, by means of a supernatant layer of liquid paraffin. The only result obtained, worthy of note, was that the spirochaetes may survive at least four days in an acid medium (0·02 per cent. HCl).

CONCLUSIONS.

From the incomplete data accumulated, it is not possible to classify the organism just described, but sufficient is known to regard it as a new species of the Spirochaetoideae. Morphologically, it resembles both the genus *Spironema* and the genus *Treponema* (as defined by Noguchi, 1918). It reacts to

Giemsa in the same way as a *Spironema* (stains bluish), but on the other hand, it is about the size of a *Treponema* and, like it, has regular spirals. Its exact position in the group must be left undetermined until more is known regarding its cultural reactions.

Of the mode of infection, nothing definite can be stated. The organism was not found below the pyloric sphincter and is certainly not passed in the faeces in a free living condition. Fleas were often found in the gastric content, but when examined microscopically (living specimens were also procured direct from the body surface), there was nothing to indicate that they were the carriers. This part of the investigation was however not sufficiently pursued to negative the "carrier" possibility. The food (fish, bread and milk) does not appear to be responsible for the infection, since animals which were recently admitted to the laboratory were fed on the same diet without being infected. Taking into consideration the length of time the infected animals had been kept in the laboratory, it seems most likely that the infection was introduced by a single animal, many months ago, and that this animal infected the others. The mode of spread from one animal to another is still to be explained.

I have to thank Professors Ashworth and Ritchie for kindly confirming my observations and for helpful suggestions. I am indebted to Professor Ritchie for the supply of some of the culture media.

The expenses of the research were defrayed by a grant from the Earl of Moray Fund of the University of Edinburgh.

SUMMARY.

1. A parasitic spiral organism averaging 4 to 8μ long, with regular, closely set spirals about 0·75μ broad, has been found in the stomach in eight cats, none of which showed any obvious signs of gastric disturbance. The organisms occurred in the lumina of ducts and glands throughout the stomach, and also within the oxyntic cells. They were not seen in any part of the intestines except the very beginning of the duodenum, or in any other organ.

2. They are extremely active, and are readily stained by aniline dyes.

3. The mode of passage from one animal to another is not known, but food and faeces may be eliminated as possible sources of infection.

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EXPLANATION OF PLATE VII.

Fig. 1. Cat III. × 1000. Polychrome methylene blue. Photograph. Section of pylorus, showing spirochaetes in the lumen of a duct.

Fig. 2. Cat I. × 1000. Drawing of selected oxyntic cells. (*a*) Oxyntic cell showing spirochaetes lying among the granules; (*b*) spirochaetes lying within a dilated canaliculus; (*c*) spirochaetes lying partly in the canaliculus and partly in the lumen of the gland.

Fig. 3. Cat IV. × 1000. Smear preparation. Alc. eosin and methylene blue. Photograph. This shows the variations in size.

Fig. 4. Smear preparation from the Dog's stomach. × 1000. Leishman. Photograph. Compare with preceding figure. Note that the spirochaetes here show larger spirals.

Fig. 5. Cat VII. × 2000. Smear preparation. Alc. eosin and methylene blue. Photograph. Spirochaetes showing chromidial granules.

Fig. 1

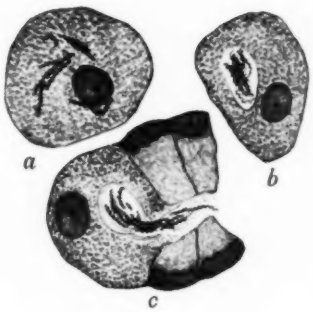

Fig. 2

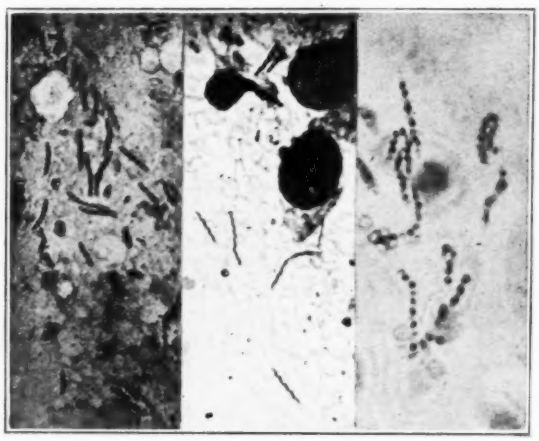

Fig. 3 Fig. 4 Fig. 5

ON A FILARIA, *LOA PAPIONIS* N. SP., PARASITIC IN *PAPIO CYNOCEPHALUS*[1].

By C. H. TREADGOLD, M.A., M.D. (Cantab.), D.T.M. (Paris).

(With Plates VIII and IX.)

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INTRODUCTION.

Before the war, the yellow baboon (*Papio cynocephalus*) was imported in considerable numbers by Dr L. C. Quéry of Paris, who organized the capture of these animals by native hunters in the interior of French Guinea and their shipment from the port of Conakry. On arrival in Paris, they were utilized by him for the production of his antisyphilitic serum. Increasing doses of a filtered broth culture of the syphilitic virus were injected subcutaneously, the baboons being killed by bleeding from the carotid artery about a month later. Having noticed the occasional presence of round worms during the operation

[1] The old name of this species, *Cynocephalus babuin*, has been condemned for reasons of priority.

of exposing the carotid artery, Dr Quéry mentioned his discovery to the late Prof. R. Blanchard, who very kindly suggested my investigating the matter. The larval and adult forms of a filaria belonging to the genus *Loa* were identified in a certain proportion of the animals examined, and the problem as to their identity or otherwise with the human parasite *Loa loa* investigated. Certain experimental researches were also initiated, but in August 1914, my work was interrupted by the war and is therefore incomplete in certain respects; I hope, however, to make good these deficiencies later. The investigations detailed in this paper were made, partly in the Laboratory of Parasitology, partly in Dr Quéry's private laboratory, in Paris.

Acknowledgments. I have to thank Dr L. C. Quéry and his staff for much kind help on all occasions; also Dr M. Langeron, whose suggestions with regard to technique were often invaluable. I am indebted besides to Prof. R. T. Leiper for several suggestions. Plate IX, fig. 3 is from a water colour by Dr E. Miller; the remainder were drawn and coloured by Madame Blanchard.

I. Description of the adult form of *Loa papionis*.

The presence of cuticular bosses in both sexes is the most obvious characteristic of the genus *Loa*. The single species hitherto recorded is *Loa loa* Guyot 1778[1]. The more important differences between this parasite and the one I am about to describe are summarized in Table I. I am inclined to think these differences justify the creation of a second species, and have accordingly named the worm *Loa papionis* after the baboon in which it was found.

Technique. The living worms were fixed in 70 per cent. alcohol at 60° C.; they were subsequently transferred to cold 70 per cent. alcohol where they were left until wanted. Before clearing, they were placed in 0·9 per cent. saline for some minutes to enable them to recover from the slight shrinkage caused by the alcohol: if this precaution be observed, the measurements made before and after fixation are identical.

The *neck* or *shoulder* described or figured by Manson (1912), Penel (1904) and Looss (1904) does not exist—at any rate in this species—provided the living worm be fixed in hot alcohol. However, this artefact is frequently visible after fixation in cold alcohol, and is no doubt produced by the contraction of the muscle cells inserted at the level of the base of the cephalic cone. In living worms an indentation appears at about this level—first on one side, then on the other—during movements of the head; it is never visible during rest.

External measurements. 12 ♂♂ and 12 ♀♀ were taken from the same baboon and measured before fixation. The ♂♂ measured 27 to 33 mm. in length, 0·4 to 0·5 mm. in breadth; the ♀♀ measured 63 to 83 mm. in length, 0·55 to 0·7 mm. in breadth. The maximum diameter is usually reached in both sexes

[1] Skrjabin (1917) describes a parasite to which he gives the name *Loa extraocularis*. However, the cuticular bosses and other characteristic features of the genus are absent from his description, which more nearly corresponds to the one usually given for *Filaria* (?) *conjunctivae* Addario.

at a point between 3 and 4 mm. behind the anterior extremity; this is maintained for a short though variable distance, after which the diameter gradually diminishes to the rounded posterior extremity. The breadth at the level of the anus is from 0·09 to 0·13 mm. in the ♂, 0·17 to 0·21 mm. in the ♀.

The figures recorded by Penel (1904), who found 34 *L. loa* at the autopsy of a negro, are of interest in this connection, and the differences between his observations and my own are brought out in Table I. In *L. papionis*, both sexes are considerably thicker and the females considerably longer than in *L. loa*; the smallest female measured by me was as long as the largest of Penel's specimens, while its maximum diameter was greater. On comparing worms of average size with one of Penel's—a female which forms part of the collection belonging to the Laboratory of Parasitology, Paris—these differences appeared very obvious.

Table I.

Summary of chief differences between Loa loa *and* L. papionis.

(*For differences in the spicules, see text, p.* 119.)

I. THE ADULTS.

External measurements in mm.

	♂		♀	
	Length	Maximum breadth	Length	Maximum breadth
L. loa (Penel's figures, 1904)	25–34	0·273–0·43	45–63	0·38–0·49
L. papionis	27–33	0·4 –0·5	63–83	0·55–0·7

Maximum thickness of cuticle in microns.

	♂	♀
L. loa Looss (1904)	9–12	9–12
L. papionis	10–12	16–20

Breadth of lateral bands in microns.

	Breadth of lateral band at base of cephalic cone	Breadth a short distance behind base	Breadth at termination of oesophagus
L. loa (Looss's figures, 1904)	♂ 9	—	63
	♀ 9	—	90
L. papionis	♂ 20–35	10–15	50–60
	♀ 40–60	20–34	80–100

II. THE LARVAE.

	Microloa loa	*Microloa papionis*
Sheath	Present	Usually absent
Measurements in microns ... (Fresh material)	210–280 × 7–7·5 Low (1911)	270–330 × 6·5–7
Shape	—	Posterior extremity rather more pointed
Subcuticular cells	Numerous	Scanty
Central viscus	Seldom seen	Frequently present
Periodicity	Diurnal	No diurnal periodicity

The cuticle and subcuticular layer. When fixed and cleared as above described, the cuticle is seen to be composed of two layers, of which the internal is thicker than the external. In the male, the internal layer shows an exceedingly fine ringed striation for the posterior 2 to 3 mm. which is visible both in the living worm and after fixation in hot alcohol; a less distinct but otherwise similar striation is sometimes to be seen in the female. The coarse striae described by Ludwig (1895) result from muscular contraction, and can be seen to appear and disappear during the movements of the living worm. They may be preserved in places after fixation in cold alcohol, but are never visible after fixation in alcohol at 60° C.

The maximum thickness of the cuticle is distinctly greater in the female than in the male: however, for *L. loa*, Penel (1904) and Looss (1904) give an identical measurement for both sexes (Table I). The cuticle is much thinner at the extremities (3 to 6μ in the ♂, 4 to 8μ in the ♀); moreover it is thicker over the anterior extremity than over the sides of the cephalic cone (Plate IX, fig. 1, *Cut.*). In the case of *L. loa*, observers are not in agreement on these points: Looss (1904) represents the cuticle as being of equal thickness in both situations, while Blanchard's drawing (1889) which is reproduced by Fantham, Stephens and Theobald (1916), more nearly corresponds to what I saw.

The cuticular bosses are very similar in appearance and distribution to those described for *L. loa*. They commence in both sexes at a variable distance behind the anterior extremity (0·71 to 2·5 mm. in the ♂, 1·2 to 3·5 mm. in the ♀). They are rather scanty in the ♂, being altogether absent from the posterior 0·54 to 1·7 mm.: numerous in the ♀, they frequently show a tendency to be concentrated in small groups, and always reach the tip of the tail or thereabouts. In both sexes the bosses vary in size in different specimens, but are always larger in the ♀ (Table II). They almost invariably look clear and structureless but I have seen the appearance of an internal papilla.

Table II.

Measurements of the cuticular bosses compared in both sexes.

		Height of bosses in microns	Diameter at base in microns
♂	No. 1	3– 6	8–14
	No. 2	3–10	8–20
	No. 3	3– 8	8–20
♀	No. 1	8–16	14–24
	No. 2	4–10	12–22
	No. 3	6–20	14–22

The size of the clear, anterior area—the so-called *cephalic cone*—(Plate IX, fig. 1, *c.c.*) varies slightly in different specimens, but in both sexes the base of the cone measures from two and a half to three times the length of the vertical diameter.

The thin subcuticular layer has the appearance of a syncytium. Its nuclei may be seen from time to time in any situation, but are especially distinct in the anterior millimetre of each lateral band, where they form an irregular double row.

The four longitudinal bands are formed by thickenings of this layer. The two lateral ones are always visible in the anterior millimetre, but apart from this are seldom very distinct; I never succeeded in tracing them the whole length of the body as Looss was able to do, moreover their breadth does not correspond with Looss's figures (Table I). The median bands are sometimes visible in the anterior millimetre; they are much narrower than the lateral bands.

The muscular system. The *muscle cells* are well developed and often show the appearance of a longitudinal striation. Those measured, varied from 1 to 3 mm. in length, by 0·03 to 0·04 mm. in breadth.

The nervous system. The anterior edge of the *circumoesophageal nerve ring* (Plate IX, fig. 1, *N.R.*) is situated about 0·15 mm. behind the anterior extremity in the ♂, and about 0·2 mm. behind it in the ♀. Its breadth is 0·03 to 0·04 mm. in the ♂, 0·04 to 0·06 mm. in the ♀. Two rounded masses containing nerve cells—the *lateral ganglia* (Plate IX, fig. 1, *L.G.*)—are sometimes to be seen embedded in its substance. Three *nerve bundles* (Plate IX, fig. 1, *N.B.*), of which the anterior is the largest, arise posteriorly on either side; they cross the body cavity and disappear in the parietes. Looss (1904) describes the nerve ring as being 0·025 mm. broad. Neither he nor other observers mention the presence of nerve cells.

The anterior papillae. The two larger ones are 8 to 10 μ in diameter, lateral to latero-median in position, and situated from 20 to 30 μ in front of the base of the cephalic cone; they have the appearance of being subcuticular, and never project above the surface; a strand of nerve fibres can sometimes be seen passing to each.

The four *submedian papillae* were never distinguished with certainty.

The digestive system. The *mouth* is a simple funnel-shaped depression in the cuticle.

The oesophagus averages 0·9 mm. in length in the ♂, 1·2 mm. in the ♀: its anterior portion is somewhat bulbous, while the diameter at the level of the constriction between the oesophagus and the mid-gut is very constantly 0·04 mm. in the ♂, 0·06 mm. in the ♀. A tube of gland substance extends from the base of the cephalic cone to the end of the oesophagus—the so-called *oesophageal gland* (Plate IX, fig. 1, *O.G.*). Circumferentially it is attached to and lies between the muscle cells, the gland substance projecting into the body cavity. These projecting masses are better developed laterally than dorso-ventrally, and are especially prominent objects just behind the base of the cephalic cone. Two ducts open into the oesophagus at the posterior border of the nerve ring, but are seldom visible.

Looss describes a large dorsal and smaller subventral glands. Other

observers simply mention the presence of glandular substance without giving any details.

The mid-gut and *rectum* correspond to Looss's description.

The ano-genital opening is 0·084 to 0·086 mm. from the posterior extremity in the ♂, while in the ♀ the anus is rather more than double this distance away.

The excretory system. I only once succeeded in finding the *excretory pore* in the ♀, and never found it in the ♂; it was situated 0·68 mm. behind the anterior extremity on the ventral surface. What appeared to be an excretory canal was sometimes visible in the substance of the lateral band.

The genital system in the male. Although a cursory examination reveals the presence of five pairs only, seven pairs of pedunculated and symmetrically situated *genital papillae* exist. The first three pairs are preanal, the last three postanal, while all six have an oval outline and diminish in size from before, backwards (Plate IX, fig. 2, $P_{1,2}$, etc.). The fourth pair are adanal in position and slender in shape. I never noticed them in undissected specimens; however, after removal of the spicules and hemisection of the posterior extremity they caught the eye at once in both cases in which this little operation was successful (Plate IX, fig. 3, P_4); in the undissected state they seem to be hidden by the spicules. The seventh pair are also readily overlooked owing to their subterminal position on the ventral surface of the sharply curved tail. If a number of living males be observed in normal saline, the tail is seen to be strongly curved in almost all of them; in fact it never seems to be completely uncoiled, although the extent of the curve may vary considerably during movement. Even after fixation in hot alcohol the curvature persists, and in several cases I was unable to see a trace of the seventh pair before dissecting the posterior extremity. Sometimes however, one or both of these papillae are quite conspicuous in the undissected state; in the first case the muscle cells were probably contracting more vigorously on the one side than on the other at the moment of fixation, the posterior extremity becoming slightly twisted in consequence (Plate IX, fig. 2, P_7); in the second case the posterior extremity was much less sharply curved than usual.

At the time, I was unable to reconcile these observations with the descriptions of *L. loa* available in the literature. Looss describes five pairs of papillae and mentions the presence of "terminal filaments" in both sexes; however, lack of material prevented him from deciding whether those of the male were distinct papillae or not. Penel (1904) records the presence of two little tubercles in this situation, as do Annet, Dutton and Elliot (1901). Penel also mentions the presence of small, adanal tubercles; but he gives no details, and does not say whether he regarded them as being constant or not. After reading Leiper's paper (1913), these difficulties largely disappear. Both Leiper and Lane regard the slender fourth pair as being bilaterally symmetrical and constant in *L. loa*; Leiper also seems to recognize the seventh pair as being pedunculated, and describes other small unpaired genital papillae in addition.

Taking everything into consideration, the number and arrangement of the paired genital papillae would seem to be identical in the two species.

The spicules (Plate IX, fig. 2, *Spic.*) differ from those of *L. loa* in being longer and broader, while the proximal ends of both are striated[1]. The appearance of their free extremities differs widely from Looss's description, but agrees in some respects with that given by Leiper.

The larger of the two, which is also the more curved, varies from 0·18 to 0·246 mm. in length. Its proximal portion is very refringent and has a coarsely striated appearance both before and after removal from the body; the non-striated terminal portion tapers towards its free extremity, which is sharply pointed. The smaller spicule varies from 0·108 to 0·13 mm. in length. Its proximal portion is not especially refringent, but shows fine, transverse striae which are only visible after the spicule has been dissected out (they are indicated for a short distance by dark shading in Plate IX, fig. 2); the terminal portion is fairly substantial and ends rather bluntly, the tip somewhat resembling the end of a crochet needle. The basal portions of both spicules appear to have a fine lumen; however, their terminal portions are not canalised but grooved, the groove extending almost to the free extremity; in the case of the smaller spicule, the proximal end of the groove shows a small fusiform dilatation.

Both these organs are contained in sheaths which open at the ano-genital orifice; they may be seen protruding for a variable distance or may be completely retracted into the body; when projecting to any extent they tend to cross one another. Retractor muscles are inserted into their bases, the spicular sheaths being lost on their outer surfaces.

The internal genitalia consist of a tubular *testis* which terminates in the *ejaculatory duct*; this opens together with the *rectum* at the *anogenital orifice*.

The nearly spherical *spermatozoa* measure from 5–7 μ in diameter.

The genital system in the female. The position of the *vulva* is relatively constant, being never less than 2 or more than 3 mm. from the anterior extremity.

The length of the *vagina* is less constant. Ludwig gave it as 3 mm. for *L. loa*. All subsequent workers give it as 9 mm. and cast much doubt upon this observation of Ludwig's. After measuring several which varied between 9 and 10·5 mm. in length, I came across one which measured only 4·2 mm., so that personally I have little doubt as to the correctness of Ludwig's statement. The upper end of the vagina divides into an anterior and a posterior *genital tube*, each of which is subdivided by Looss into *uterus*, *receptaculum seminis*, *oviduct* and *ovary*. He gives a detailed account of these structures with which my own observations entirely agree; I will not therefore describe them.

[1] In *L. loa*, striae are only described for the larger spicule.

II. Description of the ova and larvae of *Loa papionis*[1].

Technique. I shall confine myself to pointing out a few slight modifications in technique which seemed to me to increase the efficiency of certain of the methods available in 1914. For further details, see Langeron (1916).

I. *The staining of dry blood-films.* When using Pappenheim's panoptic method I obtained the best results by staining for twenty minutes with a solution of Giemsa of half the ordinary strength.

II. *Wet fixation.* Looss (1914), in describing his method, says that the film is apt to become detached if slides are used and recommends coverslips; I have not found this to be the case and prefer slides, which are easier to manipulate.

III. *Treatment after wet fixation.* Although Heidenhain's iron haematoxylin method is usually employed after wet fixation, Giemsa, Azur II, and Carbol-methylgreenpyronin also give excellent results. Preliminary overstaining, followed by differentiation with 90 per cent. alcohol, enable every detail to be seen at one stage or other of the process; moreover preparations which keep, at any rate for some months, may be made by mounting in paraffin oil and cementing the edges of the coverslip.

IV. *Mensuration.* The measuring of living embryos or larvae is rather tedious, and it was found impossible to determine their dimensions with absolute accuracy owing to the waves of contraction which are constantly passing along their bodies. However the measuring of the dead material

[1] The difficulties in the way of an accurate naming of the forms circulating in the blood, are considerable. For example, in the nematode family we are considering, it is sometimes impossible to say whether the sheath present in blood-films represents the true egg-membrane or a moult; *i.e.* we are unable to say whether the organisms in question are eggs or not. Moreover the term "*embryo*" is often used rather loosely, descriptions of sheathed and sheathless embryos being commonly met with, both in the literature and in text-books. Again, Stephens (1916) asserts that in many parasitic nematodes the young must be called "*larvae*" even before they have left the egg-shell, for they present characters which are subsequently lost. Under these circumstances conventions are essential if confusion is to be avoided. In this paper, I shall use the terms "ovum" and "embryo" so long as the existence of the egg-membrane is certain. When the membrane is absent, or when it is doubtful whether the membrane present represents a moult or not, I shall use the term "larva." In other words:

(*a*) The use of the terms "ovum" and "embryo" is restricted to the forms present in the female genital tract.

(*b*) Sheathless forms from the genital tract, together with all forms present in the blood of the definitive host, are referred to as "larvae."

Yet another difficulty occurs when the adult form is unknown. This was originally met by the coining of the term "microfilaria" qualified by some non-committal name—*Microfilaria diurna* for example. At a later period, however, *Mf. diurna* was identified as being the offspring of *Filaria loa*, while a new genus was constituted consisting of a single species—*Loa loa*. In consequence of these discoveries and changes in nomenclature, *Microfilaria diurna* is now correctly referred to as *Microloa loa*.

before fixation cannot be recommended, for a certain amount of alteration has inevitably occurred, while the extent of this will vary with the time that has elapsed since death, with the nature and temperature of the surrounding medium and so on. These difficulties are best surmounted by fixing the living material in hot alcohol, the slides being transferred to 0·9 per cent. saline for purposes of mensuration. The chief advantages of this procedure are the following:

(1) Simplicity of technique.

(2) The shrinkage that occurs is uniform and relatively slight.

(3) The taking of accurate measurements is greatly facilitated because most of the larvae are fixed in complete extension.

(4) The possibility of their dimensions being altered by complicated staining processes is avoided.

A glance at Table III shows how greatly these measurements are affected by the conditions under which they are made. Since the figures obtained from the mensuration of dried material are obviously valueless, it would undoubtedly simplify matters if those obtained after fixation in 70 per cent. alcohol at 60–65° C. and examination in 0·9 per cent. saline were stated as often as possible in addition to the figures obtained from living material.

Table III.

Measurements of Microloa loa *and* Microloa papionis *compared in microns.*

	Ml. loa		*Ml. papionis*	
	Length	Breadth	Length	Breadth
Fresh material	210–280	7–7·5 Low (1911)	270–330	6·5–7
Smears fixed wet in hot alcohol ...	208–254 Stephens (1916)	—	270–330	About 5
Dry unfixed smears treated with azur II	—	—	245–310	—
Dry smears fixed with absolute alcohol	131–166·5 Stephens (1916)	—	178–265	—

Morphology of the larvae taken from the blood. In fresh preparations, the movements of the larvae are indistinguishable from those of *Ml. loa*. After dry fixation, they are never disposed in such graceful curves as the larvae of *Filaria bancrofti*; both in thin and thick smears their attitude more nearly resembles that of *Ml. loa*, but their tails are rather more pointed (Plate VIII, fig. 1). I seldom noticed the presence of a *sheath*, although it was occasionally very distinct both in fresh and in stained preparations; as in *Ml. loa*, it is comparatively short and keeps its form during the movements of the larva.

The *cuticle* is transversely striated, and its appearance closely corresponds to Fülleborn's (1913) diagram of the cuticle in *Ml. loa*. The nuclei of the *subcuticular cells* are few in number (Plate VIII, figs. 3, 4, *N.S.C.*); I never saw

more than six or seven in the same larva, whereas Fülleborn represents forty-one in his diagram.

The anterior 7 to 10 μ is free from nuclei. In living larvae, a rather refringent terminal or subterminal granule is often visible at the anterior extremity, while an oval rather clear area, resembling a vacuole, is frequently present immediately behind it. These structures are not individualised in stained smears; however, in dried blood-films stained by the panoptic method, a central red streak or series of dots is sometimes present in this clear cephalic area.

In unfixed films stained with Giemsa, two pairs of bright-red elongated structures are often visible—one pair at each extremity (Plate VIII, figs. 5, 6, *C.B.*). Although Fülleborn describes them in *Ml. loa* and recommends vital staining with azur II and eosin for their demonstration, I never succeeded in staining them by this method; I occasionally noticed them, however, in dry films after fixation in absolute alcohol and staining with Giemsa. The column of body nuclei is separated by a space from the cuticle: the first nuclei are frequently situated in the same transverse plane, while the last one reaches the tip of the tail or thereabouts.

The *nerve ring* and the *pore-chambers* with their *pores* show nothing distinctive; in fresh material examined in a 1 in 2000 solution of azur II in 0·9 per cent. saline, the stain was observed to enter by the pores as is the case in other species.

The appearance presented by the *excretory* and *genital cells* (Plate VIII, figs. 2, 3, 4, *Ex.c.*, *G.C.*) agrees quite closely with the descriptions given by Rodenwalt (1908, 1909) and Fülleborn (1913, 1914) for the corresponding structures in *Ml. loa*. The *subsidiary genital cells* are seldom visible. The average position of the more important anatomical landmarks is given in Table IV.

Table IV.

Position of the more important anatomical landmarks expressed in percentages of the body length.

Middle of nerve ring ...	20·3
Excretory pore	30·3
Nucleolus of excretory cell	34·3
Nucleolus of first genital cell	66·5
Anal pore	81·7

In dry blood-films stained by the panoptic method, a *tail spot* is usually present immediately behind the place where the last two nuclei occur abreast (Plate VIII, fig. 1, *T.S.*).

The central viscus (Plate VIII, figs. 1, 2, 3, *C.V.*) is present in a fair proportion of the larvae and is often visible in living unstained ones. It lies a short distance in front of the first genital cell and varies up to 45 μ in length. In dried

blood-films stained by the panoptic method, it appears as a reddish granular mass, but after wet fixation the granular appearance is less in evidence; in smears treated with iron haematoxylin it appears as a siderophile body, while it stains red with carbolmethylgreenpyronin. The number of nuclei is considerably reduced in the region of the central viscus and first genital cell (Plate VIII, fig. 4); in stained preparations the resulting light area varies from 50 to 60 μ in length.

Morphology of the ova and larvae taken from the female genital tract. The ripe ovum measures about 25 by 18 μ. *The egg membrane* is secreted immediately after the entrance of the spermatozoon (Plate VIII, fig. 7, *E.M.*). At the stage of commencing differentiation the egg measures 41 by 28 μ, intermediate measurements corresponding to the morula stage. The egg grows in size up to 55 by 37 μ when the embryo commences to uncoil; the terminal flexure of the tail represents the last stage of the uncoiling process, and larvae showing this peculiarity are sometimes present in the blood-stream. Uncoiled embryos are possibly a little narrower than larvae from the blood, but their length varies between the same extremes. The egg membrane persists for a time as the embryonal sheath, but a variable proportion of sheathless larvae are present in the vagina and lower ends of the uterine tubes. I never succeeded in demonstrating the central viscus in young embryos, while it was small or absent during the uncoiling process; at this stage the anal pore chamber is not always visible, while the subsidiary genital cells are not to be seen; the nerve ring is present, but small. Little can be made out in the coiled up stage; but the excretory pore chamber is sometimes visible. Apart from such differences, all of which result from examination at an earlier stage of development, the structure of the embryos from the genital tract was identical with that of the larvae found in the blood.

The chief differences between *Microloa papionis* and *Microloa loa* are summarized in Table I.

A CONSIDERATION OF SEVERAL IMPERFECTLY SOLVED MORPHOLOGICAL PROBLEMS.

The sheath. In preparations made from the lower end of the genital tract of adult females the sheath was usually, but by no means invariably present, while it was seldom seen in blood-films. At first sight this seems rather remarkable, for the sheath appears to have been regarded by all observers as invariably present in blood-films containing *Ml. loa*. Is it possible that the presence of a sheath in *Ml. loa* is not such a constant morphological feature as it is alleged to be? The following facts would seem to be of interest in this connection:

(1) According to Stephens (1916), the uteri of *L. loa* contain eggs in the most various stages of development, besides hatched-out larvae.

(2) Brumpt (1913), remarks that in stained preparations the sheath stains poorly and therefore often appears to be absent. However, other writers do not emphasize this point, and it is certain that, on occasions, the sheath of *Ml. loa* may be very prominent in stained preparations.

(3) Manson (1912), represents *Ml. loa* as having the extremity of the tail sharply bent, while Fülleborn denies this to be the case. I seldom noticed this peculiarity in larvae from the blood, but it was frequently present in embryos taken from the female genital tract. This flexion of the tail clearly represents the terminal stage of the uncoiling process, and the microfilariae figured by Manson must be assumed to have reached the blood at a rather earlier stage than is usually the case.

On the whole, it looks as though the sheath in *Ml. loa* represents a moult rather than a persistent egg membrane in a certain proportion of cases, while statements concerning its invariable presence must, temporarily at any rate, be regarded with a certain amount of scepticism.

The buccal apparatus. The structure of the buccal apparatus—if it really exists—is most obscure. Manson (1912) gives the following description for *Mf. bancrofti.* "When the movements of the living microfilaria have almost ceased, by careful focussing it can be seen that the head end is constantly being covered and uncovered by a six-lipped—or hooked—and very delicate prepuce; moreover one can sometimes see a short fang of extreme tenuity based apparently on a highly refractile granule, suddenly shot out from the uncovered extreme cephalic end, and as suddenly retracted." Recent observers seem sceptical as to the existence of these structures. Looss (1914) frankly puts them down as optical phenomena. Fülleborn (1913) is doubtful about the existence of the prepuce and thinks the retractile appendage described by Manson was probably the upper edge of the sheath.

Personal observations. In fresh preparations I not infrequently noticed a terminal or subterminal spot or granule, together with an elongated, rather clear area behind it; this granule was often very refringent, while both it and the clear area were frequently visible in dead as well as in living larvae. In dried smears stained by the panoptic method, a central red streak or series of dots was sometimes present in this situation.

In the living larva I once observed an appearance of rhythmic movement a short distance behind the anterior extremity, but saw no denticulations. From time to time a filament appeared to be shot out and retracted for a distance of some 20 μ, while the refringent granule was a conspicuous object. On the following day, the movements were less energetic; on many occasions one filament appeared to be protruded and two retracted or vice versa; sometimes two filaments seemed to be protruded and retracted, while finally, the rounded but empty sheath was occasionally visible in front of the anterior extremity.

My final opinion is that the prepuce and filament described by Manson do not exist in *Ml. papionis*, such appearances being mere optical illusions occasioned

by the rapid movements of the larva in a sheath of low visibility. The refringent granule, together with the clear area behind it, would appear to be morphological entities, but at the present time it seems more reasonable to interpret these appearances as indicating the commencing formation of the buccal orifice and anterior part of the digestive tube, than to postulate the existence of a kind of sac from which an apparently useless filament is capable of being protruded.

The excretory and genital cells. According to the hypotheses of Rodenwalt and Fülleborn, the excretory cell gives rise to the excretory apparatus of the adult, while the first genital cell is the embryonic representative of the future genital system. Looss suggests that the accessory genital cells may give rise to the rectal ligaments and their adnexa. They and other workers assume the cellular structure of these formations to have been completely demonstrated, so before attempting to criticise the reasonableness of their belief, I will first of all describe these so-called cells as they exist in *Ml. papionis*.

Description of the excretory and genital cells. In wet preparations stained with Giemsa's solution and differentiated with alcohol, these formations are present in a considerable proportion of larvae. The excretory cell (Plate VIII, fig. 2, *Ex.C.*) is blue in colour, more or less oval in shape, and contains a darkly staining homogeneous central portion surrounded by a lighter area—the nucleus and nucleolus of Fülleborn. The blue outline is often deficient anteriorly, its lateral portions being continued forwards as two blue streaks which end at the periphery of the pore-chamber; when complete, this outline is usually continued in a forward direction as a single streak. Sometimes the cell appears to be double; frequently it is not individualised at all, its place being taken by one or more dark-blue streaks. Whether the cell is visible or not, these streaks are often continued in a posterior direction as far back as the beginning of the central viscus (Plate VIII, fig. 2, *str.*).

The first genital cell (Plate VIII, fig. 2, *G.C.*) is larger and as a rule more distinct than the excretory, measuring from 10 to 15μ in length and up to 5μ in breadth, but its shape is more variable, the ends appearing either rounded or square-cut. Often the outline of the cell is deficient posteriorly, in which case its lateral boundaries may be continued for some distance in the direction of the anal pore as an irregular double streak; when present, this outline is frequently brought into connection with the anal pore-chamber by an irregular series of blue streaks. Along these streaks the subsidiary genital cells (Plate VIII, fig. 2, *S.G.C.*) may be seen, but their individualisation is exceptional; they never exceed three in number, are quite small with a rounded outline, and contain a central darkly staining spot (Plate VIII, fig. 2, *S.G.C.*). In wet preparations stained for half an hour with carbolmethylgreen-pyronin and differentiated with alcohol (Plate VIII, fig. 4), the subcuticular and body nuclei are stained green while the excretory and genital cells are outlined in red; the central spots are stained an intense red by the pyronin and this colouration is often so marked in the case of the first genital cell as

to make its central spot the most prominent object in the whole larva; at this stage of differentiation, red streaks are to be seen between the cells and their respective pores. If the preparation be a little less differentiated, the red streaks reach from pore to pore but are absent in front of the excretory and behind the anal pore. If still less differentiated, the pore-chambers and central viscus take the red stain, and finally the pyronin predominates everywhere.

These formations are usually well shown after treatment with iron haematoxylin (Plate VIII, fig. 3, *Ex.C.*, *G.C.*). The central spot appears as a black, homogeneous body in a more lightly siderophile frame, the shape of which varies as previously described; no streaks are to be seen, while the cell outline is often feebly or not at all indicated. In dry blood-films stained by the panoptic method or with Giemsa, these cells are invisible; whilst in films stained by the panoptic method immediately after drying, the protoplasm between the body nuclei is coloured a dark green or blue in the neighbourhood of the pore-chambers (Plate VIII, fig. 1), while the pore-chambers themselves may be lightly tinted in the same way. After "vital" staining with azur II, the pore-chambers are coloured first, the excretory and genital cells next, and last of all the subcuticular and body nuclei.

Conclusions. Although I have followed the terminology of Rodenwalt in referring to the excretory and genital cells, I have only done so in order to facilitate their description. I am unconvinced as to their cellular structure for the following reasons:

(1) These so-called cells are frequently not individualised at all.

(2) When present, their outline may either be double or incomplete.

(3) I was unable to demonstrate the presence of chromatin or anything resembling a true nucleus.

An interpretation of these formations. The following facts would seem to indicate that—whatever the ultimate destiny of these formations may be—they function temporarily as part of an excretory apparatus, the products of excretion being eliminated by the pores.

(1) The presence of streaks, extending from the neighbourhood of the central viscus to the pore-chambers, along the course of which the so-called excretory and genital cells may be developed, is especially well shown on differentiating preparations fixed wet and stained with carbolmethylgreen-pyronin: moreover these formations are the last to loose the pyronin.

(2) After vital staining with azur II, the pore-chambers, together with the excretory and genital areas, are coloured before the subcuticular and body nuclei.

The central viscus. The central viscus is frequently stated to represent the remains of the vitellus and to consist of reserve material, but it does not exist in coiled embryos, and is small or absent during the uncoiling process; moreover, it is frequently small or invisible in larvae from the blood. In the

presence of these facts I am unable to support the view that the central viscus represents the remains of the vitellus.

Why this structure should be well developed in one species and poorly developed in another, is unknown. It is unknown whether the granules which enter into its composition have anything to do with the subsequent formation of the gut or not: whether they appear and disappear in a cyclical manner or whether—once formed—they persist until the larva dies or is taken up by the intermediate host, is also unknown. Under these circumstances it would seem premature to refer to these granules as consisting of reserve material.

III. General Biological Investigations.

A. Various Parasites Observed in *Papio cynocephalus*.

P. cynocephalus is a robust animal, the adult male weighing up to sixty pounds or more. *Loa papionis* was present in ten, *Microloa papionis* in twelve of the fifty-five animals examined; but no other members of the family—either adults or larvae—were discovered. At the autopsy, the internal organs always appeared healthy, although various parasites were frequently present in considerable numbers. The following were noticed at one time or another, but their identity or otherwise with known species has not yet been determined:

Plathelminths. A cestode.

Nemathelminths. *Physaloptera*, *Agchylostoma*, *Oxyurus* and *Trichocephalus*; also a small unidentified nematode from an omental cyst.

Arthropoda. The mesentery was often heavily infected with larval *Porocephalus*.

Protozoa. Protozoa were not especially looked for.

No *Plasmodia* were seen, but a small *Trypanosoma* was once noticed in a fresh preparation. It measured about 10 μ in length, while its maximum breadth was 1·5 μ. The undulating membrane was but feebly indicated and no projecting flagellum was seen; the macronucleus was a conspicuous object, being situated about the middle of the trypanosome.

An unsuccessful attempt was made to cultivate the organism in Novy and McNeil's medium. The inoculation of a small portion of clot under the skin of a mouse was also tried, but with negative results. Unfortunately the baboon had been destroyed before I thought of examining its lymphatic glands.

B. Eosinophilia in *P. cynocephalus*.

Even in the most extensively infested animals a distinct degree of eosinophilia was never encountered, the differential leucocyte counts charted in Table V being typical.

Table V.

Differential leucocyte count in six baboons examined shortly before operation. 200 cells counted.

Findings at autopsy	Polymorphs	Lymphocytes	Hyalines	Eosinophiles	Basophiles
No. 1. Marked *Loa* infection; no other parasites found	80·5	13·0	6·0	0·5	0·0
No. 2. *Loa*, *Agchylostoma*, *Physaloptera*, *Oxyurus* and *Trichocephalus* ...	54·0	31·0	12·0	2·0	1·0
No. 3. Slight *Loa* infection; many *Physaloptera*	62·5	24·5	11·0	1·5	0·0
No. 4. Many *Physaloptera* and also a *Taenia*	42·0	35·5	15·0	7·5	0·0
No. 5. Mesentery heavily infected with larval *Porocephalus*	48·0	37·5	9·0	5·0	0·5
No. 6. No parasites found	42·0	40·8	15·0	2·0	1·0

C. A Comparison of Certain Biological Phenomena in the Development of *Loa papionis* and *L. loa*.

A short account of Loa loa. This parasite has been known in equatorial Africa for hundreds of years. The adult worm is usually found under the skin, where its presence may give rise to localised and temporary oedemas—the so-called "Calabar swellings"; it is sometimes met with in the eye—more especially under the conjunctiva—and in these situations is also liable to cause local symptoms. After the death of the host it is usually met with under the skin, but has been occasionally discovered in the pericardial and peritoneal cavities; its presence in the cranial cavity has also been reported by Brunetière (1913) who suggests the possibility of its having been the exciting cause of an attack of hemiplegia. Infection in man is usually associated with a considerable degree of eosinophilia, 40 to 50 per cent. of eosinophiles being quite common. As a rule, the larvae are only found in the peripheral circulation during the daytime, but this diurnal periodicity may be lost under certain abnormal conditions. Three to four years are supposed to elapse between infection and the appearance of the larvae in the blood of the definitive host. The larvae have been shown by Leiper (1912) to undergo a further stage of development in the salivary glands of certain West African tabanid flies belonging to the genus *Chrysops*; these flies bite exclusively during the daytime.

The distribution of Loa papionis *in* P. cynocephalus. Adult *L. papionis* were found in ten out of fifty-five autopsies. Their favourite haunts were the subcutaneous tissues overlying the serratus magnus, the trapezius and the upper part of the latissimus dorsi muscles, together with the axillary folds and the region of the neck; I seldom noticed them in the inguinal or pubic regions or under the skin of the limbs, and never succeeded in finding them either in or near the eyes or in the serous cavities. However M. Bruck, who had previously performed several hundred autopsies on these animals with a view to excluding the presence of tuberculosis, etc., showed me the parasites he had found and gave me the filariae for identification. Six out of the seven

were Loas; three of them were found in the subcutaneous tissues, while the remaining three came from the pericardium, the peritoneal cavity and the upper surface of the diaphragm respectively; the seventh was found between the layers of the mesentery and did not belong to the genus *Loa*.

The distribution of Microloa papionis. When larvae were discovered in the peripheral circulation of the host during life, they were invariably present at night[1]; they were less numerous or absent in the daytime. (Table VI.)

In five animals in which the peripheral blood had been examined with negative results during life, larvae were found in the heart's blood at the autopsy. (Table VI.)

In another case, no larvae were found either during life or at the autopsy: nevertheless Dr Quéry exposed an adult *Loa* under the skin of the neck when bleeding the animal, while two more were found at the autopsy after a prolonged search. No larvae were discovered in citrated and centrifuged blood from the heart and carotid artery, and smears made from the lungs and other organs were also negative. The worms proved on examination to be full grown but unimpregnated females. These facts are interesting in that they possibly explain a point raised by Low (1913) as to the "occasional absence of larvae from human blood in cases where adult females are known to be present in the tissues."

Table VI.

The periodicity of Microloa papionis.

	Peripheral blood during life		Carotid (at operation)	Heart's blood (at autopsy)
	Day	Night		
No. 14	○*	–*	+	+
No. 17	○	+	+	+
No. 18	○	+	○	○
No. 24	+ scanty	+	+	+
No. 28	○	○	+	+
No. 31	○	–	+	+
No. 36	–	○	+	–
No. 38	+	+	+	+
No. 39	○	+	+	+
No. 42	○	–	+	+
No. 48	+ scanty	+	+	–
No. 55	+ scanty	+	–	–
Percentage of positive results	36·3	77·7	90·9	88·8

* + signs denote that *Microloa* were found, ○ signs denote negative results, and – signs indicate that no examination was made.

At the autopsy, the larvae were chiefly concentrated in the heart, lungs and large pulmonary vessels: it is possible, however, that the preliminary bleeding of the host affected their distribution to some extent. In the two animals in which a careful search was made, the distribution of the larvae was

[1] The animals were usually examined between midnight and 1 A.M.

identical (Table VII): on the whole they were most numerous in blood from the heart.

Table VII.

Distribution of larvae at autopsy—two cases.

Site	Larvae
Blood from auricles and ventricles	Numerous
Blood from large pulmonary vessels	Present in fair numbers
Smears from cut surface of lung	,, ,,
Blood from aorta	Scanty
Blood from inferior vena cava	,,
Blood from superficial vein of forearm	Very scanty
Smears from cut surface of liver, spleen and kidney	Absent

Questions arising from the absence of diurnal periodicity in Papio cynocephalus.

The liability of man to infection. Apart from cases of sleeping sickness and altered sleeping habits, the diurnal periodicity of *Ml. loa* is so marked that human infection with *Ml. papionis* would seem to be improbable.

The nature of the intermediate host. The nocturnal periodicity of the larvae suggests the transmission of the infection by a night-biting intermediate host. I had started experiments with *Anopheles maculipennis*, but they were interrupted by the war before any conclusions were reached.

The development of Loa loa *and* Loa papionis *after inoculation by the intermediate host. L. loa* is certainly a long-lived parasite, for Manson (1912) quotes a case in which the worm was extracted from the eye thirteen years after the patient had left Africa. All observers are agreed that its development must be slow, for in villages where nearly all the adults are carriers, larvae are absent in the blood of the children, although their chances of infection are presumably identical. Yet in spite of these facts, we have no detailed information as to the parts of the body inhabited by the parasite before reaching sexual maturity. I had no opportunity of examining young baboons, but never found immature Loas in the adult animals, although I was able to make detailed autopsies under the best conditions. Certainly the female Loas had not always been fertilized, but such females were approximately the same size as the rest and seemed fully developed in every respect. I shall refer to this matter again when considering the subject of immunity.

The liability of Loa papionis *to disease.* I can find no reference to diseased Loas in the literature, but they are undoubtedly liable to parasitic infections, as the following example shows: Three Loas were removed at the autopsy of a baboon in which few larvae were found during life. The peculiar dead-white appearance of one of them attracting attention, all three were kept for further examination. The opaque worm was fully as active as the other two, and all three were alive on the following day; nevertheless the opacity was due to disease. After fixation and clearing, the cuticle was still very indistinct

and covered with a fine powder which, on examination with the oil immersion, resolved itself into large numbers of small bacteria measuring about 3 by 1 μ; these were, for the most part, arranged end to end in short rows and covered a large portion of the surface of the body. The general body-cavity was packed in many places with granular débris, while the mid-gut was in a state of atony, its posterior half measuring in places more than 300 μ in diameter instead of the normal 120 to 180 μ.

The other two were also slightly infected in the same way. An attempt was made to cultivate these organisms in broth and on agar slopes, but the media remained sterile.

The absorption and calcification of dead Loas by the host. The calcification of dead Loas has been occasionally reported in autopsies on the human subject. In *Papio cynocephalus*, from 5 to 10 per cent. of the Loas found at autopsy were dead and calcified: the greatest number ever found in one baboon was forty-three, of which three had undergone this process. Whether they can be absorbed without undergoing calcification, I am unable to say.

D. The Influence of these Parasites on their Respective Hosts.

Traumatic action. In the living worms of both sexes, the mid-gut often showed through the cuticle as a bright-red streak owing to recent blood absorption; this does not seem to have been noted for *L. loa.*

Toxic action. Although no localised oedemas comparable to "Calabar swellings" were ever noticed, I am inclined to think that, in moderately or heavily infected animals, the subcutaneous fat was diminished in quantity and paler than normal. An investigation of the possible toxicity of *L. papionis* for other animals seemed therefore desirable, and the following experiments were made on guineapigs.

Experiments. Three healthy adult male guineapigs, whose blood had been examined on many occasions during the preceding three months, were chosen.

Two male and two female Loas were introduced under the skin of the back of guineapig no. I, but the stitches not being sufficiently close together, two of them escaped shortly afterwards. Two males and three females were insinuated under the skin of the back of guineapig no. II, care being taken to remedy the defect in technique. Guineapig no. III served as a control. A week later, no. II was found to be greatly emaciated, while the other two remained fat and healthy. No. II had always showed a slight lymphocytosis, and this had now become accentuated; but the percentage of eosinophiles was not increased. The animal died on the ninth day, having lost sixty grammes in weight during the last 24 hours. At the autopsy, which took place about 12 hours after death, four Loas were found out of the five which had been originally introduced. One female was discovered in the left lumbar region between the peritoneum and the muscles of the back, a second beneath the

skin of the anterior abdominal wall, while the third was lying dead in the region of the wound: of the two males, only one was found and this with some difficulty—it had hidden itself in the connective tissue between the right hamstring muscles. All fat had disappeared from the body, otherwise the organs seemed healthy. No larvae were noticed either in the peripheral blood, the heart's blood, or in smears from the various organs, but two were seen in a smear made from the connective tissue in which a female had been found; eosinophiles were not a marked feature of the preparation. The three living Loas removed at the autopsy of guineapig no. II were left for two hours in normal saline and then introduced into another guineapig.

I was unable to continue these experiments owing to the war and killed the animal the day after. All three worms were found *in situ* and their movements were as vigorous as when taken from the baboon ten days earlier. Guineapigs nos. I and III were killed at the same time. No Loas were found in no. I in spite of a careful search; they had almost certainly escaped from the wound shortly after the operation. Both animals were healthy.

Conclusions. Although the possibility of guineapig no. II having died of some undiagnosed infection was not absolutely excluded, it seems more reasonable to suppose its death to have been occasioned by the presence of the Loas.

The reaction of the host. The following facts point to the possession of a considerable, though variable, degree of immunity against *Loa* infection by the adult baboon.

(*a*) Out of the fifty-five baboons examined only thirteen (23·6 per cent.) were found to be infected.

(*b*) The degree of infection was very variable in the parasitised animals. Neither males nor larvae were present in one case; in another, forty-three Loas were found, while the blood was swarming with larvae.

(*c*) The apparent absence of immature Loas in the tissues of infected animals points to the existence of a high degree of immunity against reinfection in the adults.

E. The Treatment of Filarial Disease.

The mechanism of immunity in filariasis and the possibility of manufacturing prophylactic and curative antisera against these infections are subjects which have as yet been very imperfectly investigated in man. Yet the apparent toxicity of Loas for guineapigs, together with the undoubted immunity possessed by adult baboons against *Loa* infection, point to the production of toxin by the Loas and antibody by the host. Moreover it is possible that such antibody exists in sufficient quantity to effect a cure of *Loa* infection when baboon serum is introduced into human beings; for Quéry (1918) has recently reported the case of a patient who, after receiving a course of antisyphilitic serum, wrote to the effect that the *Loa* infection from which he had suffered up to the time of the injections, had been apparently cured by them.

Taking the known facts into consideration, it would seem as though the production of an efficient anti-*Loa* serum were possible. The subject requires investigation.

SUMMARY.

Papio cynocephalus from French Guinea frequently harbours *Loa papionis* n.sp. The intermediate host is unknown. The larvae, in contradistinction to those of the human parasite *Loa loa*, show no diurnal periodicity.

The occurrence of bacterial disease in adult *L. papionis* would seem to be a novelty; at any rate I could find no mention of diseased filariae in the literature.

In so far as the biology of *Microloa loa* is concerned, I am inclined to doubt the correctness of the opinions expressed by Rodenwalt and Fülleborn concerning the structures they term "executory and genital cells": the current hypotheses concerning the significance of these structures and of the "central viscus," clearly need revision. Manson's "buccal apparatus" would seem to be nothing more than an optical illusion, while the "neck" or "shoulder" described by the older observers as existing in adult *L. loa* after fixation, was evidently due to imperfect technique.

I have drawn attention to the desirability of standardising the technicalities which are such essential preliminaries to the accurate mensuration of microfilariae, and have suggested a method which has certain advantages over those at present in use.

Concerning the pathology of *Loa* infection, evidence both of the traumatic and toxic action of *L. papionis* on baboons, was obtained; moreover these parasites seemed definitely toxic for guineapigs, although the single experiment performed needs confirmation. The available evidence favours the supposition that adult baboons from an infected area possess a high degree of immunity both against *L. papionis* toxaemia and against reinfection by these parasites; but whether their serum is of therapeutic value for human beings infected with *L. loa*, requires further investigation.

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EXPLANATION OF PLATES VIII AND IX.

PLATE VIII.

Larvae of *Loa papionis* stained by various methods; also the ovum immediately after fertilization.

Fig. 1. The general structure of the larva is well shown but wet fixation is necessary for the demonstration of the excretory and genital cells. From blood-film stained by Pappenheim's panoptic method.

Fig. 2. Showing the streaks which connect the central viscus with the pore-chambers; also the excretory and genital cells which frequently develop along the course of these streaks. From thick blood-film fixed wet in 70 per cent. alcohol at 60° C. and stained with Giemsa's solution.

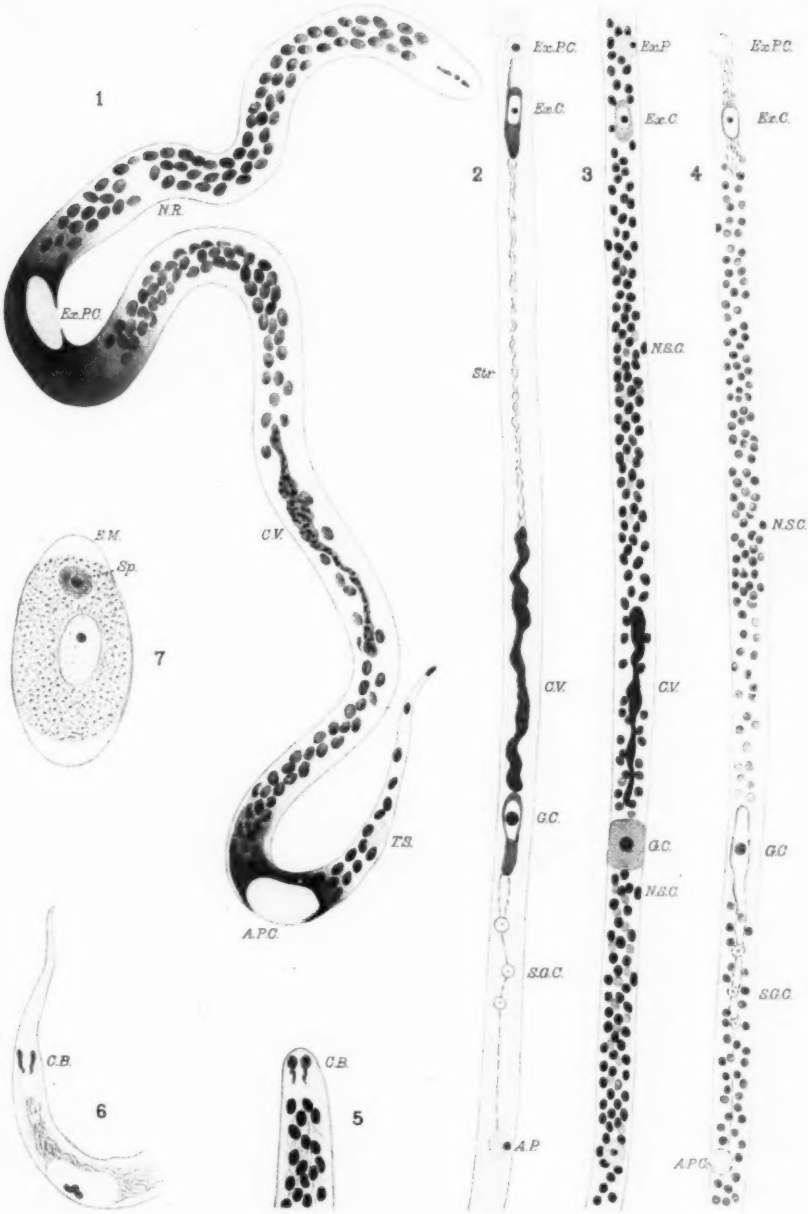
Fig. 3. Showing excretory and genital cells, pore-chambers, central viscus, nuclei of subcuticular cells, and body nuclei. From thick film fixed wet and coloured by Heidenhain's iron haematoxylin method.

Fig. 4. Owing to the absence of the central viscus, the reduction of the body nuclei in this region is very obvious. From thick film fixed wet and stained with carbolmethylgreen-pyronin.

Figs. 5 and 6. Showing the comma-shaped structures described by Fülleborn as existing at either extremity in *Ml. loa*. Fig. 5. From dry film fixed in absolute alcohol and stained with Giemsa's solution. Fig. 6. From dry film stained with Giemsa's solution without preliminary fixation.

Fig. 7. Egg from *Loa papionis* immediately after fertilization. Showing spermatozoon, and so-called egg membrane which does not exist before the entrance of the spermatozoon. From fresh material examined in a 1 in 3000 solution of Azur II in 0·9 per cent. saline.

Fig. 1 × by about 1200.
Figs. 2–6 × by about 1000.
Fig. 7 × by 1000.



Gilberte R. Blanchard, del. Cambridge University Press

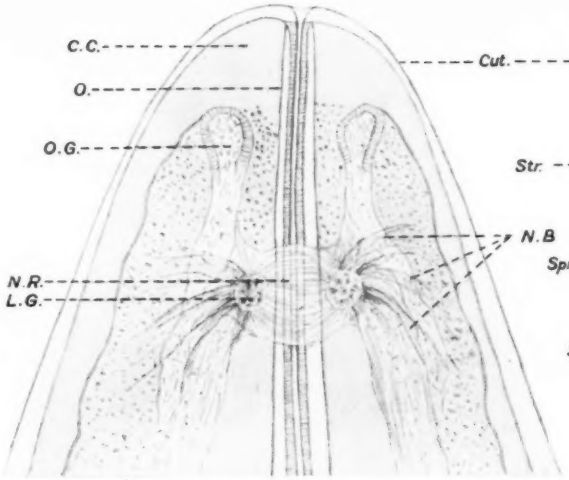


Fig. 1

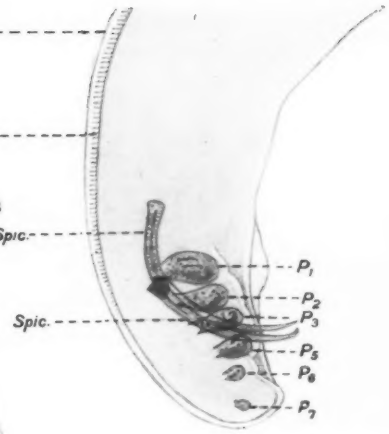


Fig. 2

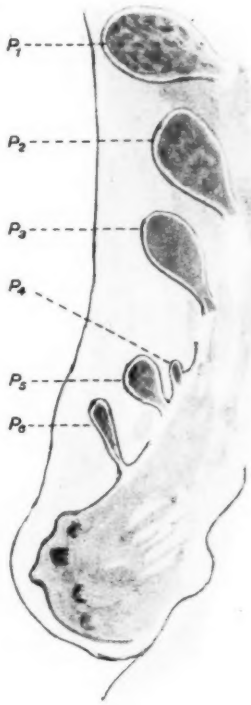


Fig. 3

KEY TO LETTERING.

A.P. = position of anal pore; *A.P.C.* = anal pore-chamber; *C.B.* = comma-shaped bodies; *C.V.* = central viscus; *E.M.* = egg membrane; *Ex.C.* = excretory cell; *Ex.P.* = position of excretory pore; *Ex.p.c.* = excretory pore-chamber; *G.C.* = genital cell; *N R.* = nerve ring; *N.S.C.* = nuclei of subcuticular cells; *S.G.C.* = subsidiary genital cells; *S.P.* = spermatozoon; *Str.* = streaks connecting excretory cell with central viscus; *T.S.* = tail spot.

PLATE IX.

Loa papionis after fixing in 70 per cent. alcohol at 60° C. and clearing in lactophenol.

Fig. 1. Anterior extremity of ♀. Showing cephalic cone, oesophagus, nerve ring and oesophageal gland.

Fig. 2. Lateral view of posterior extremity of ♂. Showing spicules and six out of the seven genital papillae on the right side; the fourth papilla is invisible.

Fig. 3. One-half of posterior extremity of ♂ after removal of spicules and hemisection. The fourth genital papilla is now visible.

Figs. 1 and 2 × by about 180.

KEY TO LETTERING.

C.C. = cephalic cone; *Cut.* = cuticle; *L.G.* = lateral ganglion; *N.B.* = nerve bundles; *N.R.* = nerve ring; *O.* = oesophagus; *O.G.* = oesophageal gland; $P_{1,2}$, etc. = first, second genital papillae, etc.; *Spic.* = spicule; *Str.* = striae.

ON FAHRENHOLZ'S PURPORTED NEW SPECIES, SUB-SPECIES AND VARIETIES OF *PEDICULUS*.

A CRITICISM OF METHODS EMPLOYED IN DESCRIBING ANOPLURA.

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(With 2 Charts.)

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INTRODUCTION.

The object of this paper is to draw attention to certain grave sources of error underlying the present mode of differentiating Anoplura[1] and more especially species of the sub-order Siphunculata. I am unable to say if the criticisms herewith advanced apply equally to the methods employed in differentiating members of the sub-order Mallophaga, because I am not familiar with the latter group, but the two sub-orders mentioned are in many respects so closely allied that it appears difficult to avoid the suspicion that the considerations herein contained may apply equally in both cases.

Fahrenholz is a recognized authority on Anoplura, he has dealt with the group in *Das Thierreich*, and consequently is in a position to mislead others who may concern themselves with the study of these ectoparasites.

[1] The order Anoplura Leach, 1817, includes two sub-orders: Mallophaga and Siphunculata (see Nuttall, *Parasitology*, XI. 332).

Until recently, owing to the war, most of Fahrenholz's publications herein referred to were rendered inaccessible to me, otherwise their consideration would necessarily have been included in my previous paper (*Parasitology*, xi. 329–346).

The subject-matter that follows has been arranged by me in three sections dealing with (1) Fahrenholz's descriptions of supposedly new species, etc., (2) my detailed criticism thereon, and (3) my conclusions therefrom in respect to the synonymy of *Pediculus humanus*.

I.

FAHRENHOLZ'S EVIDENCE IN SUPPORT OF THE VALIDITY OF HIS SPECIES, SUB-SPECIES AND VARIETIES OF *PEDICULUS*.

In considering the forms described by Fahrenholz, it appears convenient to class them in two groups:

(*a*) Lice derived from man.

Pediculus humanus race *corporis* (mihi).

P. nigritarum Fabricius 1805. Regarded by Fahrenholz as a variety (1915) and subsequently as a sub-species (1916).

P. humanus chinensis Fahrenholz 1916. A sub-species.

P. humanus marginatus (Fahrenholz 1915) Fahrenholz 1916. A sub-species.

"*P. humanus humanus* L." of Fahrenholz 1917. A sub-species.

Pediculus humanus race *capitis* (mihi).

P. capitis angustus (Fahrenholz 1915) Fahrenholz 1916. A sub-species.

P. capitis maculatus (Fahrenholz 1915) Fahrenholz 1916. A sub-species.

"*P. capitis capitis* de Geer" of Fahrenholz 1917. A sub-species.

(*b*) Lice derived from apes and monkeys.

P. schäffi Fahrenholz 1910.

P. oblongus Fahrenholz 1913, subsequently renamed *assimilis* (see below).

P. friedenthali Fahrenholz 1916.

P. lobatus Fahrenholz 1916.

P. assimilis Fahrenholz 1919 (= *oblongus* renamed).

(*a*) Lice derived from man.

In support of his contention that the lice occurring on various races of man constitute distinct sub-species, Fahrenholz (1915, p. 591 *et seq.*) cites Fabricius (1805), Olfers (1816), Denny (1842), Pouchet (1841, pp. 204–5,

quoted by Küchenmeister, 1855, p. 438), O. Fabricius (from Schiödte, 1854), Wallace (1853), Küchenmeister (1855), Murray (1861), and Lumholz (1892).

I have been able to verify the references to Fabricius, Denny, Schiödte and Wallace, those to Pouchet and Lumholz were only accessible in other editions of their works, whilst Olfers and Küchenmeister have proved inaccessible to me.

According to Küchenmeister (1855), Pouchet (1841) regarded the lice of negroes as a distinct species, but I find that Pouchet (1832, p. 412) makes no such statement. Fahrenholz cites Wallace as believing that Amazon Indian lice differ from those of Europeans, but Wallace (1853, p. 244) expresses himself cautiously, stating only that they are "probably a distinct species from that of our own country." Küchenmeister (1855, p. 428, Pl. IX, figs. 9–15) examined *nits* on the mummies of a New Zealander and Peruvian, and measured the claws of the therein contained louse embryos, finding as he supposed that they differed from those of European lice. Fahrenholz (1915, p. 593) remarks that to Küchenmeister undoubtedly belongs the credit "auf den *tatsächlich vorhandenen Längenunterschied in den Krallen der Läuse verschiedener Menschenrassen* hingewiesen zu haben[1]."

Schiödte (1854, p. 154) merely *supposed* that the Greenlander's lice, referred to by O. Fabricius, probably constituted a distinct species like those on negroes, but O. Fabricius (1780, p. 215) makes no mention, I find, of these lice being different from those on Europeans.

Lumholz (1889, p. 117, English edition) states that the head and body of most Australian natives are heavily infested with rather large dark lice that are "quite different from the common *Pediculus capitis*"; Lumholz did not become infested with the Australians' lice though they were dropped about in plenty.

We may now consider in some detail the characters which Fahrenholz, in his various publications, ascribes to the forms he distinguishes:

Pediculus nigritarum Fabricius 1805.

Synonyms:

P. nigritarum Fabricius 1805, p. 340.

P. nigrescens Olfers 1816 (*fide* Fahrenholz).

P. corporis var. *nigritarum* (Fabricius 1805) Fahrenholz 1915, p. 597, fig. 1 (sternal plate).

P. corporis nigritarum (Fabricius 1805) Fahrenholz, VII. 1916, p. 270. Designated as a sub-species for no apparent reason (*vide supra*).

[1] The italicized passages in the quotations from Fahrenholz throughout this paper are printed in spaced type by that author.

N.B. The sign ● introduced by me into citations from Fahrenholz indicates that I challenge the value of the statement he makes. Refer to my adverse criticisms as to the validity of the characters he gives in his diagnoses. See pp. 143 *et seq.*

In my previous papers, whilst I quoted Fabricius (1775 and 1794), I omitted to cite his publication of 1805 to which my attention has since been drawn by a reference of Fahrenholz's (1915). On consulting Fabricius (1805), I find that he describes lice from negroes as *P. nigritarum* n.sp., distinct from *P. humanus*:

Habitat in Nigritarum corpore. Dom. Smidt. Mus. Dom. Lund.

Paullo minor P. humano. Caput magnum, planum, laeve, triangulum, antice, subbifidum, atrum. Corpus subrugosum, atrum, immaculatum.

Therefore, as Fahrenholz notes, Fabricius appears to be the first to have regarded the lice of negroes and Europeans as distinct species. Denny (1842, p. 15) states that Latreille "designated" *P. nigritarum* as a species; Fahrenholz, however, finds no record of Latreille having created this supposed species.

Olfers (1816, Pars I, p. 81, cited by Fahrenholz 1915, p. 591) regarded lice from Ethiopians as a distinct species which he named *P. nigrescens*. Fahrenholz is almost right in regarding *nigrescens* as "doubtless" a synonym of *nigritarum*.

Fahrenholz degrades Fabricius's *nigritarum* to a variety of *corporis* and ventures to describe the variety from a *single* ♀ which he assumed represents the form named by Fabricius. Fahrenholz states that his specimen (from the Tana region) represents a distinct variety differing from negro head-lice as follows: Antennae not linear like European body-lice, but of inverted pear-shape ("umgekehrt birnförmig")●; sternum present●; the last abdominal segment bears two brown plates dorsally (as in negro head-lice)●.

P. humanus chinensis Fahrenholz 1916.

A sub-species.

Fahrenholz (x. 1916, p. 87) states of this form that it occurs on Chinese, is "*distinctly larger*"● than "*P. humanus marginatus*" (*vide infra*), and has finely dentate claws.● Of the ♂ he writes: "*schwachen Querplatten auf dem Abdomen*●, *aber auch mit gut entwickelter Genitalplatte*●. *Sternum vorhanden*●. Allgemeinfärbung bräunlich-gelb (in balsam)●.—Lebt auf Chinesen."

Fahrenholz (1917, pp. 2, 6 and text-fig., reprint) states that he identified specimens of this form at the Hamburg Museum[1]. They came from Fokim, China, and he assumes that the host was a Chinese. He comments that they are "distinctly different from those on Japanese" and gives elaborate measurements and a figure of the ♀ sternum with two hairs anteriorly but no "holes"●.

[1] The lot also contained some examples of *capitis* "die vielleicht ebenfalls einer neuen Unterart angehören" (!).

***P. humanus marginatus* (Fahrenholz 1915) Fahrenholz 1916.**

A sub-species.

Synonyms:

"*P. corporis* de Geer var. *marginatus* n.var." Fahrenholz 1915, p. 599.

P. humanus marginatus Fahrenholz VII. 1916, p. 270, and X. 1916, p. 87.

Lice from Japanese, which Fahrenholz believes to be identical with the form described by Murray (1861) as having no spine on leg I. Fahrenholz found, however, that a spine is present and was doubtless lost in the preparation of Murray's specimen. When mounted in balsam, the lice appear pale yellow●, black-brown at the sides of the abdomen●, and in places on the head●. The sternum is "totally absent●." The ♂ shows no ventral plates●; whilst of the dorsal bands only the anterior one of each segment is well developed, the posterior one being scarcely visible●; *these bands do not occur in European body-lice*●, compared to which they are somewhat smaller●. In his two papers of 1916, Fahrenholz raises his variety to the rank of a sub-species, and adds (X. 1916, p. 87): It is much smaller than the European louse● and has claw I dentate●. "Am Abdominalrande schwarzbraune Chitinleisten●. *Sternum fehlt* vollkommen●, ebenso beim ♂ die Genitalplatte●. ♂ im Gegensatz zur Europäerlaus *mit Querplatten* auf dem Abdomen●. Allgemeinfärbung gelblich●.—Lebt auf Japanern."

"*P. humanus humanus* L." of Fahrenholz 1917.

A sub-species.

This new form of terminology, for which Linnaeus need not be held responsible, is applied by Fahrenholz (1917, p. 1, reprint) to specimens in the Hamburg Museum labelled "Negerläuse aus Sansibar." Fahrenholz greatly doubts their recorded origin because they are similar to European body-lice, which, as a piece of special pleading, is difficult to match. He writes: "Der Wirt ist mir sehr zweifelhaft, da die Individuen keine Abweichungen von typischen Europäerläusen aufweisen●."

***P. capitis angustus* (Fahrenholz 1915) Fahrenholz 1916.**

A sub-species.

Synonym:

"*P. capitis* de Geer var. *angustus* n.var." Fahrenholz 1915, pp. 597–8, Pl. XXI, fig. 1 (photo of ♀), text-fig. 2 (♂ abdomen in dorsal aspect).

This form, found on Japanese, is described from balsam-mounted specimens (♂ ♀), Fahrenholz stating that the colour is distinctive●. The ♂ shows dorsal bands●, brown sternum●, and genital plate● which are absent in European lice●; claw I is longer and more curved than in the ♀, and finely toothed irregularities only occur in place of teeth●.

In his two papers of 1916 Fahrenholz raises his variety to the rank of sub-species, terming it *P. capitis angustus* in the first paper (VII. 1916, p. 270), and *P. corporis angustus* in the second (x. 1916, p. 88, *corporis* being obviously printed in error for *capitis*). To the earlier description he adds that *angustus* scarcely attains the size of European *capitis*●, but is *much narrower*, appearing much slenderer●. Claw I is very long and dentate●. "Allgemeinfärbung hellgelb●; Chitinisierung gut entwickelt; Randplatten des Abdomens tiefschwarz●. *Querplatten des Abdomens beim ♂ sehr deutlich*●; desgleichen die Genitalplatte●. Sternum vorhanden●, aber Ränder undeutlich."

Fahrenholz (1917, p. 2, reprint) refers to specimens of *angustus* at the Hamburg Museum.

Pediculus capitis maculatus (Fahrenholz 1915) Fahrenholz 1916.

A sub-species.

Synonym:

"*Pediculus capitis* de Geer var. *maculatus* n.var." Fahrenholz 1915, p. 598, Pl. XXI, fig. 2 (photo of ♀), fig. 3 (photo of ♂), text-figs. 3, 4 (♂ venter, ♀ sternum).

This form, emanating from Cameroon negroes, is described from balsam-mounted specimens (♂ ♀). The lice have a light yellow colour● in which they differ at once from lice on Japanese. Pleurae broader than in Japanese lice●. ♂ with dorsal bands dark brown●, sternum●, genital plate● and ventral band clearly defined●, four holes in the sternum bearing hairs●. ♀ with two brown spots dorsally on last abdominal segment● (as in *Haematopinus*); sternum clearly defined●, with two holes anteriorly bearing hairs●.

In his papers of VII. 1916, p. 271; x. 1916, p. 88, and 1917, p. 2 (reprint), he raises the variety to the rank of a sub-species, stating (x. 1916, p. 88) that the general form is distinctive, being shorter than "*P. capitis angustus*" (*vide supra*)●; whilst the ♀ is "*broader than European capitis*●." "Gut unterschieden durch hellbraune Grundfärbung●[1]. Chitinisierung äusserst kräftig; *vordere Randplatten des Abdomens verbreitert*●. Querplatten auf dem Abdomen des ♂ dunkel braun●, desgleichen die Genitalplatte● und *mediane Ventralplatte des II Segments* (our ventral band)●. *Sternum deutlich* gerandet●. Lebt auf Negern (Kamerun); eine etwas abweichende Form auf Hottentoten[2]."

"*Pediculus capitis capitis* de Geer" of Fahrenholz 1917.

A sub-species.

Term applied by Fahrenholz (1917, p. 2, reprint) to specimens in the Hamburg Museum identified by Fahrenholz as such.

[1] Light yellow in his first description, light brown in his second.

[2] Another Fahrenholz variety which no doubt will presently be described.

(*b*) Lice derived from apes and monkeys.

***Pediculus schäffi* Fahrenholz 1910.**

This form was described by Fahrenholz, 1910, p. 57, Pl. III, figs. 2, 6, and text-fig. 1 (eggs); host: *Simia troglodytes*. The species was condemned and "regarded provisionally" for reasons specified by me (*Parasitology*, XI. 336–7) as = *P. humanus* race *schäffi* (Fahr.). I see no reason to change my opinion.

***Pediculus friedenthali* Fahrenholz 1916.**

The author states (X. 1916, p. 88) that this form occurs on *Hylobates mülleri*. He only describes the ♀ which "much resembles the head-louse of man." After dwelling on trivial points of detail he adds:

"Sternum fehlt●...*grösste Breite im V Segment*●...*Letztes Segment des* ♀ *breiter als lang*● so dass die Gonopoden in den Einschnitt desselben hineinragen. *Gonopoden sind nach hinten gerichtet* und stehen der Form nach in der Mitte zwischen denen von *P. capitis* und *P. humanus*●."

***Pediculus lobatus* Fahrenholz 1916.**

This form was named by Fahrenholz in 1913 (p. 373) but not described, the host being given as *Ateles pan*. Fahrenholz (X. 1916, p. 89) afterwards named the host *Ateles rellerosus* (sic) and described the louse (♂ ♀) as follows:

"Kopf ähnlich dem von *P. capitis*. Vorderkopf an den Seiten je eine dunkelbraune Platte●. Sternum fehlt●; Thorax ohne Borsten●; Abdomen sehr breit, mit tiefen Einschnitten (besonders beim ♀). ♂ mit zweiteiliger Genitalplatte (wie bei *P. capitis maculatus*)●. Letztes Segment des ♀ hat statt Ausschnitt nur einen feinen Schlitz●."

Prior to seeing the foregoing description, I had concluded (X. 1919, pp. 337, 340) that the form probably represents *P. humanus* race *capitis*. The description merely confirms me in this belief. Several lots of lice that I have examined from different species of *Ateles*, cannot, I find, be differentiated from ordinary *capitis*.

***Pediculus assimilis* Fahrenholz 1919.**

Synonym:

P. oblongus Fahrenholz 1916.

This form was named by Fahrenholz in 1913 (p. 373) but not described. He gives the hosts as *Hylobates concolor* (*mülleri*) and *Symphalangus* (*Hylobates*) *syndactylus*. Fahrenholz (X. 1916, p. 88) gives the host as *Hylobates syndactylus* Desm. and describes the ♀ only. Omitting the trivial details he gives, the diagnosis mentions the following supposedly specific characters:

"grösste Breite im VII Segment●...*Gonopoden* in Form denen voriger Art gleichend; die *nach innen gerichteten Spitzen* erreichen nicht den Einschnitt● des *letzten Segments, das in Länge und Breite gleich ist*●."

Fahrenholz (1919, p. 27) renamed the form *assimilis* finding the name *oblongus* preoccupied. This form was regarded by me (x. 1919, pp. 337, 340) as probably *P. humanus* race *capitis*, and I am confirmed in this belief by the foregoing diagnosis which has since become accessible.

II.

EVIDENCE DISPROVING THE VALUE OF THE CHARACTERS WHEREBY FAHRENHOLZ DISTINGUISHES THE BEFORE-MENTIONED FORMS OF *PEDICULUS*.

Of the older authors who have examined lice obtained from different races of man, Murray (1861), whom I have cited elsewhere (II. 1919, p. 206), did not venture to regard such lice as belonging to distinct species. He does not, however, distinguish clearly between head-lice and body-lice in reaching his conclusions. Piaget (1880, p. 623), who regarded *corporis* and *capitis* as separate species, in referring to the latter, fully appreciated its variability, for he wrote:

"Il ne me semble pas qu'il faille attacher beaucoup d'importance à ces différences. En examinant un plus grand nombre d'individus de la même race, il en sera probablement comme de ce que j'ai eu sous les yeux. Quelques individus avaient le côté interne de la griffe dentellé, d'autres entièrement lisse; la couleur passait du gris au jaunâtre. C'était le cas chez les parasites d'Européens et de Malais faisant partie de ma collection. Du reste, je ne vois pas que l'on puisse tirer de ces minimes différences quelque argument pour ou contre l'unité d'origine des races ou espèces humaines."

Neumann (1910, p. 411), who also quotes the foregoing passage from Piaget, lays stress on the need of examining many adult lice from various races of man before reaching conclusions. Having examined many such specimens, he concluded that "les transitions sont insensibles entre la forme type (européene) et les diverses formes exotiques et que l'on est porté à les réunir toutes en une espèce unique." The pigmented chitinous structures which possess great taxonomic value in Anoplura, correspond in lice from negroes "à des renforcements chitineux, incolores ou peu colorés chez le pou de l'Européen. Il en résulte que *P. capitis* est infiniment mieux caractérisé par les spécimens des races noires...."

It is remarkable that Fahrenholz should attach importance to the superficial statements of the earlier authors I have cited on p. 137 and not have taken a warning from the writings of vastly more careful observers like Murray, but especially Piaget and Neumann, whom I have just quoted.

The subject of the relation between *capitis* and *corporis* has already been discussed at length by me (*Parasitology*, XI. pp. 339 *et seq.*) and I see no reason to modify my statements in view of those of Fahrenholz's publications which have since become accessible to me in the original. I was thinking not only of Fahrenholz but also of others when I stated (*Ibid.* p. 333) that "Such

studies require the use of other methods than the usual one of treating specimens with caustic potash and mounting them in balsam." Fahrenholz's purported species of *Pediculus*, *i.e. schäffi*, *lobatus* and *oblongus* (= *assimilis*) were degraded by me (*Ibid.* pp. 334–340), the first to a race of *P. humanus*, whilst the others were merely regarded as probably forms of the variable race *capitis*. Of Fahrenholz's varieties of "*P. capitis*," *i.e. maculatus*, *angustus* and *marginatus* (since raised to the rank of sub-species by that author), I ventured "to assert that these names will not stand and that they will fall into the synonymy of *P. humanus*," also that they "are surely based on faulty observation." Already in an earlier paper (II. 1919, p. 208), referring to the three above-mentioned varieties, I wrote: "Judging from Fahrenholz's other publications to which I shall refer elsewhere (meaning here), this author has also in this instance merely burdened science with three names which will fall into the synonymy of *Pediculus humanus*." That these comments were justified is proved by the following detailed criticism dealing with (*a*) the measurements, (*b*) morphology and (*c*) pigmentation of *Pediculus* and their bearing on the forms which Fahrenholz has attempted to define.

(*a*) Measurements of *Pediculus*.

There are certain sources of error that cut at the base of all measurements made on lice, and these require consideration because they have been widely ignored: (*a*) When lice die and dry up, the soft parts of the integument shrivel so that the insects shrink considerably. The antennae become shortened, the hard parts, this being especially evident in *capitis*, becoming partly telescoped into each other. The neck-like portion of the head is retracted into the thorax, the abdomen collapses and may shorten greatly. (*b*) When dried lice are placed in water their soft parts imbibe the fluid and the body resumes its normal contour, but by placing them afterwards in alcohol whose strength is gradually increased, such previously dried specimens may be made to retain their normal external form. (*c*) When dried specimens are placed in 10 per cent. caustic potash their bodies imbibe fluid and become swollen to the limit of their capacity if the exoskeleton is uninjured. (*d*) When fresh or dry caustic-treated specimens are cleaned and mounted in balsam, they frequently collapse again more or less provided extra precautions are not taken; therefore measurements made on balsam-mounted specimens are fallacious in most cases.

When living or well preserved lice are examined, it is evident (*e*) that the amount of food they have imbibed alters their dimensions and (*f*) that the number of eggs contained in the body of the female distinctly alters the length and width of the abdomen. Moreover, (*g*) the head protrudes more from the body of fully fed lice than from those that are unfed or but partly fed.

As an example of the effect of feeding upon the body-length I cannot do better than cite an observation by Sikora (IX. 1917, p. 276) who measured two females before and after feeding, the result being more striking in the

case of *corporis* because of its habit of gorging (see Nuttall, *Parasitology*, XI. 343–344): Sikora found *capitis* when unfed measured 2·84, fully fed 2·92; *corporis* when starving measured 3·2 by 1·4, fully gorged 3·84 by 1·56 mm.

Finally, owing to the lack of sharply defined structural demarcations, it is difficult to measure the length of the head, thorax and abdomen (especially its segments) more than approximately. Therefore little value necessarily attaches to small differences in size, and seeing that *Pediculus* varies considerably in size, measurements can have but small importance unless applied to a large number of full distended specimens assuming that these are obtainable.

With regard to the width of the abdomen, Fahrenholz states that it is greater in his "*P. capitis marginatus*" than in "*P. capitis angustus*" whose abdomen is elongated, and that the greatest width is attained at the "7th segment" in *assimilis* and at the "5th segment" in *friedenthali*[1].

The value of Fahrenholz's statements bearing on the width of the abdomen is nil, because I have often detected elongated, broad, and intermediate forms of abdomen in both sexes where I have examined large lots of *capitis* and *corporis* that have been collected from single individuals in different parts of the world. Pure strains of *corporis*, raised in the laboratory, have yielded a like result. Moreover, as with the length, the width of the abdomen in both sexes varies according to the state of engorgement, and in females according to the number and size of the ova they contain. Thus in laboratory strains of *corporis* I find that the greatest width ranges forward and backward from the 4th, 4th–5th and 5th abdominal segments (the 5th = Fahrenholz's "7th") in the ♂, whilst in the ♀ the greatest width alternates between the 3rd–4th, 4th, and 5th abdominal segment, the latter most frequently attaining the greatest width (abdominal segment 3 = Fahrenholz's "5th").

For the reasons previously given, no value can be attached to Fahrenholz's statement that the last abdominal segment in "*P. assimilis*" ♀ is equally long and broad, such measurements being fallacious especially in balsam-mounted specimens.

Following the lead of many previous authors, Fahrenholz lays stress on the relative size of *capitis* and *corporis* and of his purported new forms. Examined critically, however, in the light of the subjoined table, these differences should be seen once and for all not to hold good. I have stated this repeatedly in a general way but the appended table will perhaps carry more conviction.

Dismissing the measurements of *capitis* and *corporis* given by older writers, as perhaps wanting in accuracy, I have arranged the following table of measurements by recent authors and newer measurements of my own in accordance

[1] The reader is liable to be confused by Fahrenholz's enumeration of the segments. He does not state that he includes segments 1–3 in the thorax. What *appears* to him and most observers to be the 1st abdominal segment is numbered 4 by Fahrenholz, but it actually consists of two fused segments (abdominal segments 1 and 2) which bear the first abdominal spiracle. Fahrenholz when he refers to segments 5–6–7 must therefore, in the light of our present knowledge, be understood to refer to abdominal segments 3–4–5 which bear correspondingly numbered abdominal spiracles.

with the size of the males, beginning with the smallest. Where measurements of males are lacking, those of the females are ranged in what appears to be a suitable place. In some of Fahrenholz's measurements I have omitted the second decimal figure. I omit so-called "average" measurements given by different authors, recording only those showing the range in size, smallest to largest, observed in both sexes. Apart from my hitherto unpublished figures, those of Sikora bearing on *capitis* are the only ones regarding which a statement is made as to the number of individuals measured.

Table.

Giving the body-length of the smallest and largest specimens of different forms of *Pediculus humanus* measured by various observers and the author. My measurements were made on well-preserved alcohol specimens.

Length of ♂ in mm.	Length of ♀ in mm.	Name	Number examined	Author and remarks
2·0 –2·7	2·4 –3·4	*capitis*	104 ♂ 123 ♀	Sikora, IX. 1917
2·1 –2·3	2·3 –2·8	"*capitis maculatus*"	?	Fahrenholz, X. 1916, "shorter than *angustus*"
2·1 –2·6	2·2 –3·3	*capitis*	85 ♂ 81 ♀	Nuttall, Lot 208, woman, Cambridge
2·1 –2·8	2·2 –3·7	*corporis*	27 ♂ 77 ♀	Nuttall, Lot 204, woman, Lambeth
2·1 –2·8	2·4 –2·9	*corporis*	137 ♂ 94 ♀	Nuttall, Lot 265, Lab. Stock
—	2·19–2·85	"*friedenthali*"*	?	Fahrenholz, X. 1916. Host: *Hylobates*
2·19–2·39	2·67–3·06	"*capitis angustus*"	?	Fahrenholz, X. 1916, "scarcely as large as European *capitis*"
2·2 –2·3	—	*capitis**	3 ♂	Nuttall. Hosts: *Ateles ater* and *geoffroyi*
—	2·4 –2·66	"*assimilis*"*	?	Fahrenholz, X. 1916. Host: *Hylobates*
2·2 –2·5	2·4 –3·3	*capitis**	7 ♂ 11 ♀	Nuttall, Lot 315. Host: *Ateles paniscus*
2·25–3·0	2·75–4	*capitis*	?	Popoff, 1916
2·35–2·9	2·6 –3·3	*corporis*	31 ♂ 100 ♀	Nuttall, Lot 314, tramp, Cambridge
2·43–2·56	2·61–3·1	*capitis*	?	Fahrenholz, 1912
2·5 –2·9	3 –3·3	"*humanus marginatus*"	?	Fahrenholz, X. 1916
2·55–3·3	2·85–3·7	*corporis*	56 ♂ 52 ♀	Nuttall, Lot 212, London
2·7 –3·55	2·7 –4·2	*corporis*	220 ♂ 226 ♀	Nuttall, Lot 252, tramp, Cambridge
2·74–3·6	2·74–4·4	*corporis*	?	Sikora, IX. 1917
2·75–3·75	3 –4·75	*corporis*	?	Popoff, 1916
—	3·29–3·36	"*schäffi*"*	?	Fahrenholz, 1912. Host: *Simia troglodytes*
2·9 –3·3	3·9 –4·37	"*humanus chinensis*"	?	Fahrenholz, X. 1916, "distinctly larger than *marginatus*, the largest larger than European louse" (*vide infra*)
3·02–3·23	3·55–4·20	*corporis*	?	Fahrenholz, 1912 (European no doubt)
3·75	4 –4·5	*capitis*†	2 ♂ 2 ♀	Popoff, 1916, from Java

* Denotes forms found on apes and monkeys. I have measured two "*schäffi*" ♀♀, both 3·3 mm. in length. (Fahrenholz, 1910, gives 2·7 as the length, I assume his later statement to be correct.)

† If correctly determined, the size is remarkable. Thus far, in a very large material, I have seen no *capitis* approaching these in size.

The accompanying Chart II, moreover, records measurements made by me on 100 ♀♀ *P. humanus* race *corporis* (Lot 252, from tramp, Cambridge, 1918). The measurements relate to the antennae, head, thorax and abdomen as indicated on the chart, all being arranged along a straight line representing the anterior margin of the thorax. The lice were graded in accordance with the size of the thorax, the largest on the left leading to the smallest to the right. The length of the thorax varied between 1·1 and 0·7 mm. which may be taken as a good index of the relative variation in size in the lot. The great inequality in the length of the abdomen is due to its being more or less filled with blood

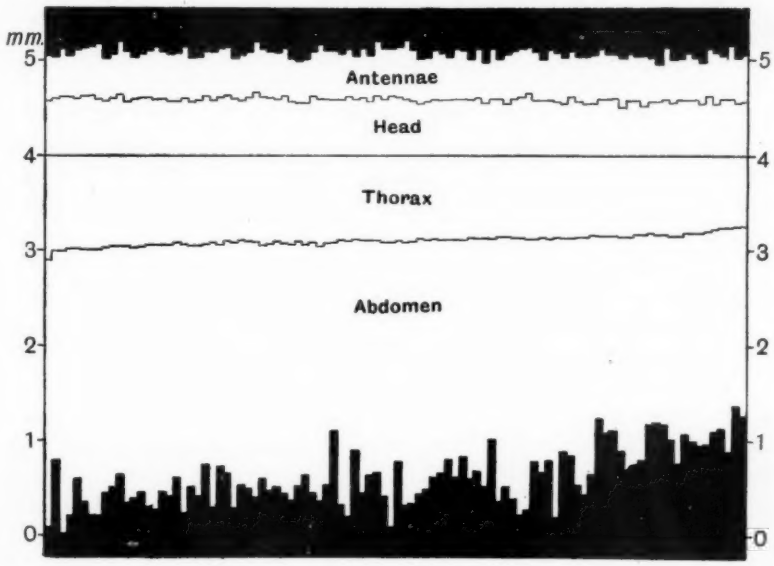

Chart I. Length-measurements of *Pediculus humanus* race *corporis*, 100 ♀♀, arranged in accordance with the length of the thorax.

and ova. The variation in the length of the head and antennae is relatively slight though distinct.

(*b*) Morphology of *Pediculus*.

The morphological characters and their bearing on Fahrenholz's diagnoses will be considered in sequence, beginning with the head and ending with the legs:

HEAD. There is no doubt that in *capitis* the head is shorter than in *corporis* when *typical* forms are considered. The shortness in *capitis* is due to the more blunted shape of the clypeus which terminates the head anteriorly, and the less elongate form of the neck-like posterior portion. Nevertheless, in pre-

sumably pure breeds of *capitis* and *corporis* respectively, the form of the head varies so that its taxonomic value is largely vitiated. In cross breeds a complete series of intermediate forms may be observed.

ANTENNAE. The statement that *capitis* has shorter antennae than *corporis* likewise holds for typical forms. In presumably pure breeds, a distinct variability is however noticeable, and in cross breeds all kinds of intermediate forms of antennae are seen. In pediculi derived from apes and monkeys, the antennae, like the head, are of the *capitis* type.

In body-lice from negroes ("*P. nigritarum* Fabricius") Fahrenholz describes the antenna as inverted-pear-shaped, the author apparently meaning to refer to the form of the segments composing the antenna, but his wording implies that the whole antenna has this form, this being absurd. He only describes the form from a single ♀ which may well have been a *capitis* with collapsed antennae.

THORAX. It is difficult to define the shape of the thorax dorsally because the outer margin is virtually colourless and the pigmented portions which lie within the margin mislead the eye into accepting them as indicating the form of the thorax. Its shape varies slightly in individual specimens, the lateral contours being more or less convex.

Therefore, when Fahrenholz describes the shape of the thorax in "*P. capitis angustus*" as "parallel sided," in dealing especially with balsam-mounted specimens, the supposed character must be dismissed as valueless. The six large hairs situate dorsally on the thorax in all pediculi I have examined, are stated to be absent in "*P. lobatus*" but I firmly believe that they were merely overlooked by being viewed through balsam (see further under Pigmentation).

ABDOMEN. Fahrenholz, writing of the ♂ abdominal structures, refers to what we have termed the dorsal bands, genital plate, and anterior ventral band. His statements regarding these structures are largely controverted in the following section on Pigmentation, *q.v.*

The Genital plate, in the ♂, is stated by Fahrenholz to be bipartite in "*P. lobatus*" and "*P. capitis maculatus*," and absent in other pediculi. We have, however, shown that this structure varies in normal individuals of one lot (see Keilin and Nuttall, *Parasitology*, XI. 282, fig. 3) and consequently there is no significance to be attached to its consisting of one or two parts, whilst it is never absent.

In the ♀, the *posterior abdominal lobes*, when retracted, become approximated, giving the semblance of a slit in contrast to the usual bilobed appearance of the end of the abdomen when the lobes are protruded. This accounts for what Fahrenholz gives as a specific character in "*P. lobatus*."

The *gonopods*, in the ♀, are stated by Fahrenholz to point back in "*P. friedenthali*," inward in "*P. assimilis*," and to be "short" in both forms, being intermediate in shape between those of *capitis* and *corporis*. I find, however, as already stated elsewhere (Nuttall, *Parasitology*, XI. p. 341), that the form of the gonopods is inconstant in both of these races of *P. humanus* and that

the two forms cannot be distinguished by their gonopods. As to the gonopods pointing "backward" or "inward," this is frequently due to pressure or shrinkage, such abnormal orientation being often seen in balsam mounts.

In both sexes, the *pleurae* vary greatly in appearance according to the degree of chitinization and pigmentation. There is no constant difference between *capitis* and *corporis* in this respect, but in "*P. schäffi*." the 6th abdominal segment certainly projects in an exceptional manner, forming a ridge dorsally and ventrally which is especially evident in ungorged specimens. The 6th abdominal segment does not protrude exceptionally in the adult lice I have examined from monkeys, but it protrudes distinctly in 2nd and 3rd-stage larvae. In corresponding larval stages of human *capitis* it is exceptional to find the 6th abdominal segment protruding somewhat more than the others laterally.

CLAWS. These are described by Fahrenholz as longer or shorter in lice from different races of man, as toothed in "*P. capitis angustus*" and "*P. corporis marginatus*," but not toothed in European lice. These statements are untrue, for the claws vary in length normally and I have often seen toothed claws in European head and body-lice. See also the quotation from Piaget (p. 143).

(*c*) Pigmentation in *Pediculus*.

The worst blunders committed by Fahrenholz are due to his relying upon pigmentation in his diagnoses, this leading to his referring to various structures as "absent" in some pediculi and "present" in others. Thus

The HEAD in "*P. lobatus*" has dark brown "plates" at the sides.

THORAX. Here the *sternal plate* is said to be present in "*P. corporis nigritarum*" and "*P. capitis angustus*" and "absent" in "*P. lobatus*" and "*P. friedenthali*." In "*P. capitis maculatus*" there occur "holes" in the sternum where hairs arise anteriorly, there being four holes in the ♂ and two in the ♀ sternum.

ABDOMEN. The degree of pigmentation of the *pleurae* serves to distinguish "*P. capitis maculatus*" and "*P. capitis angustus*."

In the ♂, the *dorsal bands* are present in "*P. corporis marginatus*" and "absent" in European body-lice. The *genital plate* is present in "*P. capitis angustus*," "*P. capitis maculatus*" and "*P. humanus chinensis*," but "absent" in European lice. The ventral band is a feature in "*P. capitis maculatus*."

In the ♀, on the last abdominal segment, there occur two brown spots dorsally in "*P. capitis maculatus*," indistinct plates (dorsally?) in "*P. capitis angustus*," and two brown plates in "*P. corporis nigritarum*" (based on one ♀!) and negro head-lice.

It is surprising that Fahrenholz should have been so grossly misled. He might at least have taken a warning from Neumann's paper (see quotation on p. 143). Today we know that by raising unpigmented strains of European *P. humanus* on a black background, the "absent" structures of Fahrenholz

are rendered visible even in balsam-mounted specimens! Fahrenholz merely overlooked existing structures because they were unpigmented. Conversely, by raising pigmented lice on white backgrounds, all of Fahrenholz's specific characters may be made to disappear.

Nearly all of the before-mentioned structures in *Pediculus* are illustrated in *Parasitology*, XI. p. 220, Pl. X, figs. 1 and 2 (pigmented and unpigmented specimens raised on black and white respectively), pp. 281 *et seq.*, figs. 2, 3. Others will be considered shortly in papers dealing with our studies on the anatomy of the insect.

It is obviously fatuous for Fahrenholz to describe colour differences in balsam-mounted specimens of lice derived from various races of man ("*P. capitis angustus*" and "*P. capitis maculatus*").

How much he was misled by preconceived notions regarding the different appearances observable in *P. humanus*, is further exemplified by the circumstance that when he found typical *P. humanus* race *corporis* in the Hamburg Museum collections bearing a label stating that they came from negroes, he considered their origin as "very doubtful." He would not believe that negro clothes-lice could be similar to those of Europeans, hence there must have been an error in the labelling (see p. 140). I have many hundreds of specimens which prove that body-lice from negroes and whites are identical in appearance.

Proof that there is no constant relation between the degrees of colouration shown by different parts of the exoskeleton in pigmented P. humanus.

The following observations were made by me with a view to determine if in a series of more or less pigmented specimens the colouration of the various parts follows any uniform law.

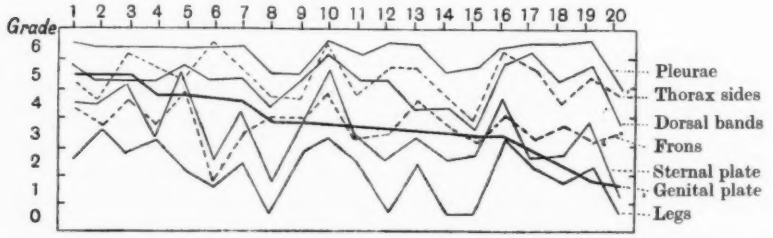

Chart II. Recording the variation in pigmentation shown by 20 selected *Pediculus humanus* race *capitis*, ♂♂, arranged in accordance with the degree of pigmentation shown by the genital plate which is darkest (*i.e.* Grade 5) in specimen 1 and palest in specimen 20, as indicated by the heaviest line among the curves.

From several hundred *capitis* ♂♂ (Lot 252, well-preserved), collected from a negro's head in Tropical Africa, 20 specimens were chosen which showed various degrees of pigmentation when viewed by daylight whilst immersed in alcohol in a dish. A scale giving seven grades of colour from blackish brown

(Grade 6) down to practically colourlessness (Grade 0) was painted on paper with water-colours, and the various degrees of pigmentation exhibited by the lice were recorded on a chart with the aid of the colour scale. The specimens were at first charted in no particular order, but afterwards they were ordered in accordance with the degree of pigmentation shown by their genital plates. The results of this colorimetric study are shown in the accompanying Chart II wherein the thickest line among the curves records the gradual fall in the degree of pigmentation shown by the genital plate in 20 ♂♂. It will be noticed at once that the degree of colouration of the genital plate bears no relation to that of the other structures. This plate may even be colourless whilst all the other structures are distinctly pigmented. The degree of pigmentation appears fairly uniform in the pleurae, whilst in some other structures (*i.e.* frons, sides of thorax, etc.) it often rises and falls, sometimes synchronizing with the varying colouration of other parts and sometimes not. In short, there is often agreement but no constant relation between the degrees of pigmentation shown by the different parts.

These observations bear on my criticism of Fahrenholz's work in so far as they prove that considerable individual variation may occur in the degree of pigmentation shown by different parts of the exoskeleton of *Pediculus* and that this has to be taken into account in all descriptions.

III.

SUPPLEMENTARY NOTE UPON THE SYNONYMY OF *PEDICULUS HUMANUS*.

The following synonymy requires to be added to that supplied in my previous paper in *Parasitology*, XI. pp. 334–7:

(*a*) *Pediculus humanus* race *corporis*.

1805. *Pediculus nigritarum* Fabricius 1805, p. 340. From negroes.

1816. *Pediculus albidior* Olfers 1816, p. 81, cited by Fahrenholz, VII. 1916, p. 270.

1816. *Pediculus nigrescens* Olfers 1816 (*fide* Fahrenholz, *loc. cit.*).

1910. *Pediculus capitis vestimenti* Neumann 1910, p. 412. "Il me paraît logique de conclure qu'il conviendrait de faire descendre *P. vestimenti* du rang d'espèce à celui de sous-espèce et de le considérer comme *P. capitis vestimenti*." This procedure is not permissible under the rules of zoological nomenclature, for *humanus* has priority over *capitis* as a specific name and *corporis* has priority over *vestimenti* as a sub-specific varietal, or racial name.

1915. *Pediculus corporis* var. *nigritarum* (Fabricius 1805) Fahrenholz 1915, p. 597, fig. 1.

1916. *Pediculus humanus chinensis* Fahrenholz X. 1916, p. 87. From Chinese.

1916. *Pediculus humanus marginatus* (Fahrenholz 1915) Fahrenholz VII. 1916, p. 270. From Japanese.
1916. "*Pediculus corporis nigritarum*" of Fahrenholz VII. 1916, p. 270.
1917. "*Pediculus humanus humanus* L" in Fahrenholz 1917, p. 1 (reprint).

(*b*) *Pediculus humanus* race *capitis*.

1816. *Pediculus pubescens* Olfers 1816, p. 81, cited by Fahrenholz, VII. 1916, p. 270.
1916. *Pediculus capitis angustus* (Fahrenholz 1915) Fahrenholz X. 1916, p. 88. From Japanese.
1916. *Pediculus capitis maculatus* (Fahrenholz 1915) Fahrenholz VII. 1916, p. 271. From Negroes.
1916. *Pediculus friedenthali* Fahrenholz X. 1916, p. 88. From *Hylobates mülleri*.
1917. "*Pediculus capitis capitis* de Geer" in Fahrenholz 1917, p. 2 (reprint).
1919. *Pediculus assimilis* Fahrenholz, 1919, p. 27 (= *P. oblongus* Fahrenholz renamed).

CONCLUSIONS.

The evidence adduced in this paper points to the imperative necessity for the employment of more scientific method in the description and differentiation of species of Anoplura. It is shown that a leading authority on the group has blundered greatly in dealing with *Pediculus*, and this may be taken as a fair example (compare *Haematopinus*, etc.) of the manner in which many purported species, sub-species and varieties of Siphunculata are being foisted into the literature by that author. Surely it is time to call a halt to this unwarranted process of burdening science with useless specific and other names that are destined in many cases to fall into synonymy.

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ON TWO NEW GREGARINES, *ALLANTOCYSTIS DASYHELEI* N.G., N.SP., AND *DENDRORHYNCHUS SYSTENI* N.G., N.SP., PARASITIC IN THE ALIMENTARY CANAL OF THE DIPTEROUS LARVAE, *DASYHELEA OBSCURA* WINN. AND *SYSTENUS* SP.

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(With Plate X and 2 Text-figures.)

1. *ALLANTOCYSTIS DASYHELEI* n.g., n.sp.

The host of this gregarine is the larva of a Ceratopogonid: *Dasyhelea obscura* Winnertz, which, as I have previously mentioned[1], lives in the decomposed sap filling the infected wounds of the Elm and Horse-chestnut trees in Cambridge (at Newnham and along the Queen's Road). The parasitised larvae were found late in the season, about the end of September, they were all young and never heavily infected, containing from three to eight and exceptionally twelve parasites in different developmental stages. The gregarine seems to be rare as among several hundred of these larvae examined only twelve yielded this interesting parasite.

All the stages of *Allantocystis dasyhelei* occur in the midgut of its host, in the space between the intestinal epithelium and the peritrophic tube, and they always lie with their main axis parallel to that of the larva.

The full-grown sporont is elongated, 65–75 μ long and 20–22 μ across its widest portion (Pl. X, fig. 3). The sporont moves slowly and its body easily bends on meeting an obstacle. The ectoplasmic layer is very thin except anteriorly. The endoplasm is very granular and completely masks the nucleus, which can be detected, however, by compressing or staining the parasite; the nucleus then shows a structure typical of gregarines, *i.e.* a large vesicle with a distinct karyosome. The youngest stages of the parasite observed were the sporonts, 25–35 μ in length, differing from the full-grown forms only in having their endoplasm less granular and in containing several patches of very small yellowish granules (Pl. X, figs. 1 and 2). In sexual association the gregarines attach themselves to one another by their anterior extremities.

[1] See D. Keilin, *Parasitology*, this volume, p. 85.

So far, the characters of this gregarine agree with all we know of the general structure of the group. The peculiar character of the species is confined to the structure of its cyst. It is well known that in gregarines two full-grown sporonts (or gametocytes), when associated for reproduction, contract their body and form a more or less spherical mass which is surrounded by a common cyst.

In the case of *Allantocystis dasyhelei*, on the contrary, the two sporonts associated for reproduction, without changing their form, secrete a very elongated sausage-like cyst[1], measuring 140–150 μ in length and only 20 μ in width (Pl. X, fig. 4).

Once the cyst is formed, the protoplasm slightly retracts, the septum which previously separated the two gametocytes disappears, and the interior of the cyst forms a fused mass consisting of dark granular protoplasm with irregular contours. The gametes and the sporoblasts seem to be formed by the ordinary process common to almost all gregarines. In a few cases I could follow *in vitro* the formation of the sporoblasts; a freshly formed cyst (similar to that represented in Pl. X, fig. 4) left in normal salt solution at 7.15 p.m. one day, was found at 10 o'clock the next morning with completely formed sporoblasts as represented in Pl. X, fig. 5.

The sporocysts (Pl. X, figs. 6 and 7) are spindle-shaped, with one side slightly more prominent than the other; they are 18 μ long and 6·5 μ wide.

It is important to note here that the only gregarine known, where sporonts do not contract their body before sporulation, is the very interesting form found by Léger (1892, pp. 159–160) in the coelom of the Polychaete worm *Glycera*, and described by him under the name *Ceratospora mirabiles* Léger. This gregarine, however, differs from *Allantocystis* and all other known gregarines in a very important character, namely, the associated sporonts remain always separated from each other by a septum, and the gametes of each sporont develop parthenogenetically into spores. It would be of great interest to study cytologically the development of these spores, but unfortunately, as Léger mentioned, this gregarine is rare. The peculiar shape of the cysts of *Allantocystis* makes it difficult to define the systematic position of this genus.

DENDRORHYNCHUS SYSTENI n.g., n.sp.

This gregarine was found in a larva of a Dolichopodid fly: *Systenus* sp., probably *Systenus scholtzii* Loew[2], which occurs with the larva of *Dasyhelea obscura* Winn. in the decomposed sap of the Elm tree; but, while the latter larva is saprophagous and feeds upon decomposed sap, the larvae of *Systenus*

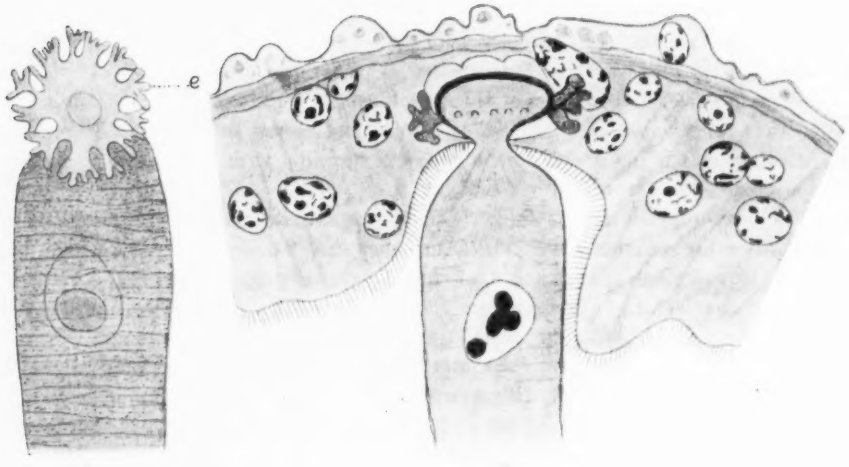
[1] Whence the generic name *Allantocystis*.

[2] The host was kindly identified by Mr C. G. Lamb as belonging to the genus *Systenus* being probably *S. scholtzii* Loew, but for the exact identification of the species it is important to examine the ♂♂, which unfortunately I failed to obtain. The ♀ of this species is difficult to distinguish from that of *S. adpropinquans* Loew whose larvae were found by Laboulbène (1873) in the sap of the Elm tree.

is carnivorous and lives upon *Dasyhelea* and several other dipterous larvae which are always found associated.

The gregarine, in different stages of its development, occurs only in the midgut of its host, where it can remain for a long time as a trophozoite, attaining, at this stage, the size of a full-grown sporont, *i.e.* being 255 μ long and 18·5–20 μ wide.

In all the stages the gregarine moves very slowly and easily bends and contracts its body (Pl. X, figs. 11 and 12), which looks often as if it were composed of numerous rings; these curved specimens can frequently be seen performing a continual rotating movement. The epimerite of the cephalont

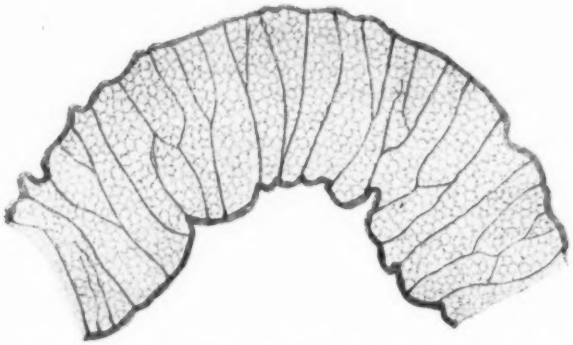


Text-fig. 1. *Dendrorhynchus systeni: A*, the anterior portion of a trophozoite showing the epimerite (*e*). *B*, section of a trophozoite with its epimerite fixed in the epithelium of the host's midgut.

(Text-fig. 1, *A* and *B*) has the form of a disc surrounded by numerous more or less ramified papillae.

At various stages, the cephalont, shedding off the epimerite, can separate itself from the host's epithelial cell and become a free moving sporont (Pl. X, figs. 8, 9 and 10). The body of the sporont is elongated with the posterior end slightly curved and of irregular contour; it does not seem to be divided into two segments, pro- and deutomerite, as is usual in cephaline gregarines. The ectoplasm is not very thick and shows well the longitudinally striated epicyte. The living, and especially the fixed and stained specimens, show, under the epicyte, a network of very well defined circular fibrils with oblique anastomoses which surround the whole body of the gregarine (Text-fig. 2). They undoubtedly correspond to the myocyte fibrils of *Gregarina munieri* described by Schneider (1875), although in this case the network is much

denser than that of *Dendrorhynchus*. In some specimens of *Dendrorhynchus* it was rather difficult to ascertain that the transverse fibrils were only superficial and did not penetrate deeper in the endoplasm and form a series of septae similar to those of *Taeniocystis mira* described by Léger (1906). The endoplasm is very granular, the granules being disposed in transverse parallel planes. The vesicular nucleus, with usually several karyosomes, is situated in the anterior portion of the gregarine. I have not yet been able to find the sexually associated forms, though several times I found the subspherical cysts, 60 to 80 μ in diameter, but unfortunately none of these cysts showed the spores. On the other hand in several young *Systenus* larvae, containing the trophozoites of *Dendrorhynchus*, I found the cysts of elongated shape, about 100 μ long, measuring 40 μ across their widest portion and having one side prominent and the other flattened (Pl. X, fig. 13). These cysts, which probably belong to the same gregarine, contained ripe spindle-shaped spores 18–19 μ long and 7 μ wide (Pl. X, figs. 14 and 15).



Text-fig. 2. *Dendrorhynchus systeni*: a portion of a trophozoite fixed and stained, showing myocyte fibrils.

The shape of the epimerite of this gregarine recalls that of *Rhopalonia stella* Léger and *Echinomera hispida* (Schneider) Labbé, and I am inclined to think that the genus *Dendrorhynchus* can be placed near the latter two genera in the family of DACTYLOPHORIDAE Léger (1892).

It is interesting to note that the *Systenus* larva, the host of *Dendrorhynchus*, often contains a Schizogregarine bearing much resemblance to *Schizocystis gregarinoides* Léger (1910), which, with *Taeniocystis mira* Léger (1906), live in the larvae of *Ceratopogon soltitialis*.

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EXPLANATION OF PLATE X.

All the figures were drawn from living specimens.

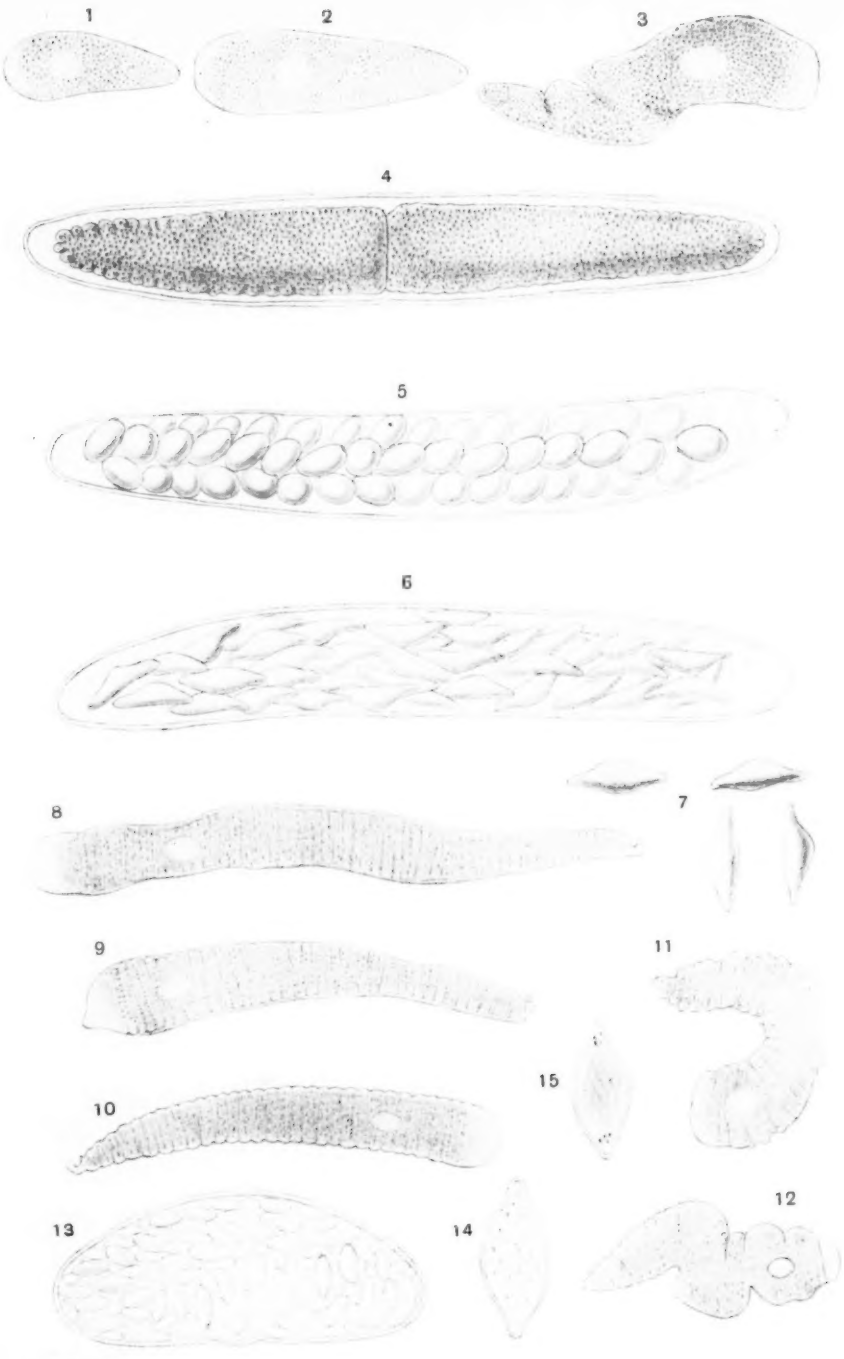
Allantocystis dasyhelei. ×800.

Figs. 1 and 2. Young sporonts.
Fig. 3. Full grown sporont.
Fig. 4. Cyst freshly secreted by a copula; the thickness of the cyst-wall is exaggerated.
Fig. 5. Cyst with formed sporoblasts.
Fig. 6. Cyst with spores.
Fig. 7. Spores seen from different sides.

Dendrorhynchus systeni. Figs. 8–12. × 490.

Figs. 8, 9 and 10. Different stages of sporonts.
Figs. 11 and 12. Contracted sporonts.

Fig. 13. Cyst with spores, probably belonging to *D. systeni*. ×490.
Figs. 14 and 15. Spores of the same cyst. ×1000.



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SPERMATOGENESIS IN *IXODES RICINUS* LINN.

By ERIK NORDENSKIÖLD, Stockholm.

(With Plate XI.)

It has long been known that ticks possess spermatozoa that differ considerably from the typical flagellate form. In similar cases science has always attempted to trace the aberrant type back to the normal with a view to identifying its constituent parts. Many forms, even those which at first sight appear incapable of being compared with the normal, have recently been thoroughly analysed in this manner. On the other hand there occur several types of spermium whose parts it is impossible to compare with those of the normal type and in these instances all that can be done is to identify the elements that take part in the fertilization, viz. the nucleus and centrosome.

Very little has previously been published on spermatogenesis in ticks. A. Bonnet (1907) refers to it and Samson (1909) has published a preliminary note on the subject whilst Robinson and Davidson (1914) refer but briefly thereto. None of these publications fulfils the demands of a modern investigation of spermatogenesis; neither as regards terminology, nor in the attempt to trace the development of the different elements is any attention paid to former scientific results on this subject. Under these circumstances it is scarcely possible to discuss the details of these papers; some of the stages described in them can by the aid of the figures be put into their proper places, others are impossible to identify.

In an earlier paper (1909), I described the results of some of my researches on spermatogenesis in *Ixodes ricinus*[1]. The present paper contains several corrections relating to statements made in my previous communication, these corrections being based upon more detailed investigations that have thrown new light on several matters. The earlier results were obtained chiefly from material fixed in Carnoy's alcohol-chloroform-acetic acid. Meanwhile it has been proved that this method, excellent as it is for several other purposes, is very unsuitable for studies on spermatogenesis. The results described in the present paper were obtained mainly from material fixed in Flemming's chromosmic-acetic acid, due attention always being paid also to the Carnoy-material.

Since my earlier paper appeared, our knowledge of spermatogenesis and its accompanying phenomena has considerably increased. Several matters,

[1] Nordenskiöld (1909). Zur Spermatogenese von *Ixodes reduvius*. *Zoologischer Anzeiger*, XXXIV. 511–516, 10 figs. (*Ixodes reduvius* Latreille, 1844 = *Ixodes ricinus* Linn. 1758.)

i.e. the conjugation and the reduction of the chromosomes, have become special subjects for investigation and such researches are becoming increasingly specialized, because they demand specially adapted material and a great sacrifice of time.

Owing to lack of opportunity for the complete elucidation of the various problems concerned in spermatogenesis, and the *Ixodes* material not being very suitable for the purposes of investigation, I shall deal summarily with certain aspects of the subject and confine myself here to tracing the changes that are undergone by the young spermatid whilst developing to the full-grown spermatozoon.

The spermatogonium. Among the elements of the testis the spermatogonium is, as usual, the smallest (Pl. XI, fig. 1); its plasma is homogeneous, finely granular, without any distinct inclusions; its nucleus is relatively large, spherical, with a large nucleolus, a fine and close linin-network, and, scattered over this, a very finely granular chromatin. At the mitosis, this substance forms 28 short, slightly curved, rod-shaped chromosomes. The centrosome appears at the division as a very conspicuous, triangular corpuscle; but as will be shown, it is hard to follow its later development. The spermatogonial divisions appear in the earlier part of the nymphal stage at a time when the whole gonad still forms a narrow tube with homogeneous contents. The later development of the gonad cells appears, on the other hand, only at the beginning of the last moult before the prosopon stage.

The spermatocyte. The resting spermatocyte of the first order (Pl. XI, fig. 2) shows a round or, when pressed by crowding, a somewhat angular shape. The globular nucleus forms the largest part of the cell. It shows a well-developed linin-network, on which the chromatin is scattered in the form of slender threads. The nucleolus is large and the nuclear membrane thin. The surrounding plasma has a double structure: the inner zone around the nucleus is uniformly fine-granular and contains larger or smaller aggregations of mitochondria. Around this inner zone is seen an outer layer, somewhat resembling a zona pellucida, and composed, as a closer investigation will show, of a denser and more deeply staining matrix, through which extends a system of diffuse less deeply staining processes from the inner plasma. The resting spermatocyte of the second order differs from that of the first order only by its smaller size.

The spermatid is, as usual, smaller than the spermatocytes. Beginning with the telophase of the second maturation division (Pl. XI, fig. 3) there is seen, along with the redissolving chromosomes, the centrosome closely attached to the nucleus, often hidden among the chromosomes, and always as a matter of fact, opposite the spindle. The spermatid, when full grown (Pl. XI, fig. 4), shows a nucleus with generally the same arrangement of chromatin and achromatin as in the spermatocytes, for it shows a reticular linin and, scattered in it, a granular chromatin; the nucleolus is conspicuous by its size, and is indeed far more voluminous than in the former cells. The

plasma has also the same arrangement of its chief components: the outer layer has the same fibrillar structure as previously described in the spermatocytes; it is however much thicker in comparison with the inner layer; the latter also shows the same granular substance and the same aggregations of mitochondria around the nucleus.

The further development of the spermatid begins, as usual, with a change in the position of the nucleus which moves through the plasma to the periphery and becomes closely attached to the cell membrane (Pl. XI, fig. 5). Here it must be observed that the final position of the nucleus depends on that of the spindle of the last division: the nucleus always passes to the side where the remains of the spindle appear as an appendix to the plasma (Pl. XI, fig. 6). This circumstance makes it possible to follow the different constituents of the spermatid during its subsequent intricate process of metamorphosis.

The above-mentioned change of place is the signal for a series of modifications in the shape of the nucleus. At first its constitution is altered: its several components, linin, chromatin and nucleolus seem to be effaced and to emerge as a homogeneous, uniformly colourable matter. This substance shrinks and becomes concentrated towards the inner part of the nuclear vesicle (Pl. XI, fig. 5), the outer part being occupied only by nuclear fluid; later on the nuclear membrane shrinks round the substance, thus considerably diminishing the volume of the nucleus. There now begins a still more important change in the shape of the nucleus: first it becomes somewhat pear-shaped, later on it elongates and becomes rod-shaped (Pl. XI, figs. 6 to 12). In transverse sections this nuclear rod (Pl. XI, fig. 9) shows a peculiar structure, owing to the disposal of the chromatin in peripheral longitudinal filaments surrounding a central chromatin cord. In order to define the orientation of the rod, the exterior end, which is turned towards the fragment of the spindle, will be termed hereafter the external end, and the opposite end will be called the internal end.

During this nuclear process important changes are taking place in the plasma: (1) *the endoplasma*. Here the mitochondria, which, as is shown above, were crowded around the nucleus in the form of several well-circumscribed masses, are dispersed homogeneously through the whole endoplasma (Pl. XI, figs. 4, 5), and at this stage it is impossible to discern them as a special ingredient of this matter. Through this dissolution of the mitochondria the endoplasma itself acquires a greater affinity to stains, which characterizes it during the following stages. Round the external end of the nucleus the endoplasma penetrates through the ectoplasma and here appears at the surface of the cell (Pl. XI, figs. 8, 10, 11). At the opposite side it also expands and forms a very characteristic process, at first obtusely conical (Fig. 8), which later on comes to play a very important part in the development. Even more remarkable are the changes in (2) *the ectoplasma*. The original fibrillar structure of the plasma-zone disappears; the fibrils melt away and simultaneously the whole layer increases considerably in thickness. In the now nearly homogeneous layer, appear several large vesicles, distinguishable

from the surrounding plasma by their clearer contents and increasing greatly in size (Pl. XI, figs. 11, 13, 14). Among these vesicles one especially, situated opposite the internal end of the nucleus, attains a considerable size (Fig. 15). Finally the vesicles run together and occupy the whole mass of the ectoplasma; they are, as this shows, also plasma structures and not liquid inclusions.

The part played by the centrosome during this evolution of nucleus and plasma is not yet described. When last seen, it was at the telophase of the second maturation division, half hidden among the chromosomes at the part of the cell opposite the spindle. The most difficult part of the whole investigation was the subsequent following of the centrosome. The very important part it plays everywhere in the development of the spermatozoon makes an accurate observation of it through the several phases of the cell-metamorphosis indispensable. One meets indeed not infrequently with investigations on spermatogenesis wherein the centrosome has been invisible at some stage, and in which its behaviour is only traceable by inference. Such is also unfortunately the case with our subject. In the meta- and ana-phases of the mitoses the centrosomes are easy to observe as triangular points, surrounded by a strong radiation, but, already at the telophase, the centrosome, as has been explained, is not always easy to find. And in the young spermatids it is generally very difficult to distinguish the centrosome from the similarly granular mitochondria: none of the special staining methods recommended in the literature for this purpose was of any use here, although many have been tried; the mitochondria cannot be decolourized in such a way that the centrosome remains, nor is this element, as is very often the case in other objects, surrounded by any characteristic plasmatic structure such as radiation or clear plasma zone, which could be used as a means of identification. On close examination it is indeed possible to fix the position of the centrosome at least approximately. Here the telophase must be the starting point. In it the centrosome lies, as has been already mentioned, close to the chromosomes and always at the pole of the nucleus opposite to the mitotic spindle. At this pole there is, even after the reconstruction of the spermatid nucleus, in favourable preparations, a minute deeply coloured structure, which must undoubtedly be identified with the centrosome (Fig. 3). As the nucleus begins to approach the spindle side of the cell surface, and later on becomes rod-shaped, it is to be expected, that the centrosome would even still be found at the internal end of the nucleus. As a matter of fact, at this place, in many preparations, can be seen a very small, deeply staining granule (Fig. 7), which may be regarded as the centrosome. In the following stages the centrosome unites even more closely with the internal end of the rod-like nucleus (Figs. 10–12, 14). It appears in close union with the end of the nucleus, surrounded by a clear zone, and opposite the previously mentioned conical projection of the endoplasma.

In the following development the nucleus, the centrosome and the mitochondria of the endoplasma play the most considerable part and consequently

these three parts of the spermatid must be specially studied. This development is characterized by a still more considerable elongation of the nuclear rod. The internal end of it begins to bend in various directions (Figs. 12–16). The external end of the nucleus also assumes a characteristic shape, its point becoming bluntly elongated, almost club-shaped (Figs. 15–18). This end retains its position at the surface of the nucleus, and forms the fixed point, round which the other parts of the nuclear rod move; the latter is sometimes **S**-shaped, sometimes spiral-shaped. As development proceeds the rod becomes progressively thinner and more convoluted.

Parallel to this development of the nucleus there are equally important changes in the plasma. The endoplasma, as we left it, when it had reached the cell membrane in the neighbourhood of the external end of the nucleus, extends its surface from this point and grows in this way all around the ectoplasma (Figs. 10, 12, 16–18). And at the same time the above-described endoplasmatic projection, opposite the internal end of the nucleus, penetrates deeper into the ectoplasma and assumes a more pointed shape (Figs. 14, 15, 17). In the protuberance there accumulates a considerable quantity of mitochondria from the endoplasma, the whole projection acquiring a deep colour (Fig. 17). With this mitochondrial body the internal end of the nucleus enters into a relation, thus making it most difficult to observe the development of the centrosome in the phase that now follows.

As the internal end of the nucleus begins its movements, the centrosome follows them. It is often seen in the first stages of the bent nucleus at the concave side of the rod, the concavity of which seems to be occupied by the clear zone round the centrosome (Figs. 11, 12). Later on the centrosome seems to become attached to the end of the nucleus and surrounded by a now very diminished clear zone (Fig. 14). Thus situated, it follows for a while the movements of the nucleus as shown by Fig. 16. But after this it is soon lost to sight. At the same time we see that the end of the nucleus extends into the mitochondrial body of the endoplasma (Figs. 15, 17) and therefore we may conclude that at this phase the centrosome leaves the nucleus and remains among the mitochondria. It is not possible to adduce any strict proof of this statement, since, as is mentioned above, it is impossible to decolourize the mitochondria in a way that leaves the centrosome stained. Nevertheless this supposition is very probable. The loosening of the connection between nucleus and centrosome happens at the same time as the nucleus and the mitochondria come into contact, moreover, the mitochondrial body in the succeeding development plays a part scarcely intelligible without assuming union with the centrosome. This being the case it will be assumed in the following that the above statement is correct.

The next stage of the spermatogenesis effects an ejection of a part of the plasma such as very often follows the transformation of the spermatid to spermatozoon. It begins with a considerable expansion of the plasma-vesicle (Pl. XI, figs. 17–19), leading to the formation of a large sac of ectoplasm from

the wall of which the endoplasm, with the contents of the more or less coiled nucleus, centrosome-body and mitochondria, protrudes as a cap-shaped boss. The plasma ejection begins with the formation of a protuberance from the endoplasm (Pl. XI, fig. 20 *a*), at first conical, later increasing considerably (Figs. 20 *b* and *c*); lastly it separates itself from the same plasma body and forms a tail-shaped appendix fastened to the external end of the nucleus (Figs. 20 *b*, 21–23). This end of the nucleus pushes itself entirely outside the cell, the curved internal end of the nucleus alone remaining in the plasma and in this way keeping up the connection with the original plasma and the tail-shaped part of it. This tail has originally a purely plasmatic character, being formed of an internal, granular, mitochondrial cord, covered by a quite thin hyaline plasma-layer (Figs. 21, 22)[1]. After a while this conformation alters: it now forms a hollow tube through which several deeply-staining filaments pass, and is attached to the now funnel-like end of the nucleus (Figs. 23, 24). From the bottom of the funnel a thin cord is stretched along the whole appendix. Lastly the whole tail shrinks and assumes the form of a knotted thread, which finally vanishes entirely (Fig. 24). This process thus forms a plasma ejection of the sort that has been observed very commonly in the spermatogenetic development.

During this development of the nuclear appendix the cell plasma undergoes equally remarkable changes. The ectoplasma-vesicle, rounded at the beginning (Figs. 18, 19), grows in length, at first assuming a club-like and later a rod-like shape (Figs. 21, 22), and at the same time the centrosomal corpuscle—this name seems suitable for the centrosome with surrounding mitochondria—passes from the endoplasma to the ectoplasma, where it takes its position near the boundary between the two (Fig. 24). The endoplasma, which was formerly gathered together in a solid mass, spreads in an ever thinner layer over the rounded front end of the ectoplasma-rod leaving the centrosomal corpuscle at the point of the rod (Pl. XI, fig. 24).

The movements of the nucleus continue during these changes in the plasma: as the endoplasma still has its compact form, the nucleus is seen situated either at right angles to the plasma-rod or as a continuation of it (Figs. 22, 23). Later on, when the endoplasma has spread, the nucleus is situated on the surface of the plasma-rod (Figs. 24, 25, *a*, *b*) and begins finally to roll itself up at its anterior end (Fig. 26), but stretches out again along the side of the plasma-rod. At the same time the centrosomal corpuscle becomes conical in shape and assumes a position at the end of the plasma-rod in close contact with the end of the nucleus, as shown in Fig. 31, and in transverse section in Fig. 27.

Behind this centrosomal cone there now appears along the centre of the plasma-rod a stainable central cord (Figs. 26, 30, 31), the origin and signifi-

[1] This can be specially shown by material fixed with Flemming's liquid. On Carnoy-material the tail shows from the beginning a sort of skeleton-structure. Unfortunately I have got no commencing stage of the tail-formation in Flemming-material.

cance of which are two of the most difficult problems in the whole investigation. The fact is that at the stage in question there appear in the plasma-rod longitudinal folds, which are more colourable than the plasma itself, and as it seems, at least in some transverse sections, are formed by invagination of the surface (Figs. 28, 29), from which it seems possible to conclude, that the cord mentioned above is formed in this way, by folding and separation of the fold from the surface. The spermia, which are always curved and folded, here prevent to a very great extent the observation of the process, but cross-sections, as mentioned above, make this interpretation of the conditions at least possible.

Through the definitive location of the nucleus along the plasma-rod and the appearance of the above-mentioned cord the spermatozoon acquires the shape shown in the vas deferens of the male (Figs. 30, 31). At this stage we see the rod-like, laterally placed nucleus, the conical centrosomal corpuscle, united with the nucleus, the plasma-rod with its staining cord. The spermatozoon of the tick is, as shown by this, atypical, and, like that of several crustaceans, cannot be compared with regard to its several components, with the common spermatozoon type. A desire to attain this object led me astray in my preliminary investigation, but the errors in my previous publication can easily be rectified by the results published here.

The work, of which the results are herein published, was begun at the Zoological Laboratory at Marburg and finished after a long interval of time at the Zoological Institute at Christiania. To Professors Korschelt and Tönniges at Marburg and Bonnevie at Christiania I am much indebted for the helpful advice I have received during my work, for which I here beg to offer them my most respectful thanks.

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Note:—From the extensive literature on spermatogenesis may here be quoted only some authors that have been especially consulted in connection with the work, the results of which are here described; a great many others, that have only occasionally been consulted, may from considerations of space be omitted.

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EXPLANATION OF PLATE XI.

The figures have been drawn with an apochromatic Zeiss lens 2 mm., and a compensation ocular No. 8 (tube-length 160 mm.), giving a magnification of 1000 diameters; they were projected on the working table through a camera of Abbe's model. Figs. 1–5, 20, 23 and 27 were drawn from preparations fixed in Carnoy, the others from Flemming preparations. Heidenhain's iron-alum haematoxylin was used as a stain throughout.

Fig. 1. Spermatogonium in resting-phase.

Fig. 2. Resting spermatocyte of first order.

Fig. 3. Telophase of second maturation division, with centrosome and remnant of spindle.

THE SPERMATID.

Fig. 4. Resting phase.

Fig. 5. Showing contraction of nucleus.

Fig. 6. The same, with remnant of spindle visible.

Fig. 7. Elongating nucleus, centrosome, and thickening of ectoplasm.

Fig. 8. The nucleus has assumed a rod-shaped form, vesicles are appearing in the ectoplasm and the endoplasm shows aggregations of mitochondria, and conical protrusion.

Fig. 9. Nucleus seen in transverse section.

Figs. 10–11. Successive developments of nucleus; centrosome visible.

Fig. 12. The same, showing endoplasm growing round ectoplasm, and appearance of metachondrial bodies.

Figs. 13–15. Showing convolution of the nucleus, enlargement of the ectoplasm-vesicles, and further development of the mitochondrial body.

Fig. 16. Showing growth of endoplasm round ectoplasm.

Fig. 17. The same, the centrosome at extremity of nucleus.

Figs. 18–19. Showing expansion of the ectoplasm-vesicle, and the protuberant mass of endoplasm containing the coiled nucleus and mitochondrial body.

DEVELOPMENT OF THE SPERMATOZOON.

Fig. 20 *a*, *b*, *c*. Phase of plasma expulsion and formation of tail-shaped appendix.

Figs. 21–22. Showing the plasma appendix separating from the cell body, elongation of ectoplasm-vesicle, and nuclear changes.

Fig. 23. The plasma appendix begins to disappear.

Fig. 24. The endoplasm forms a thin covering to the ectoplasm, with mitochondria between the two.

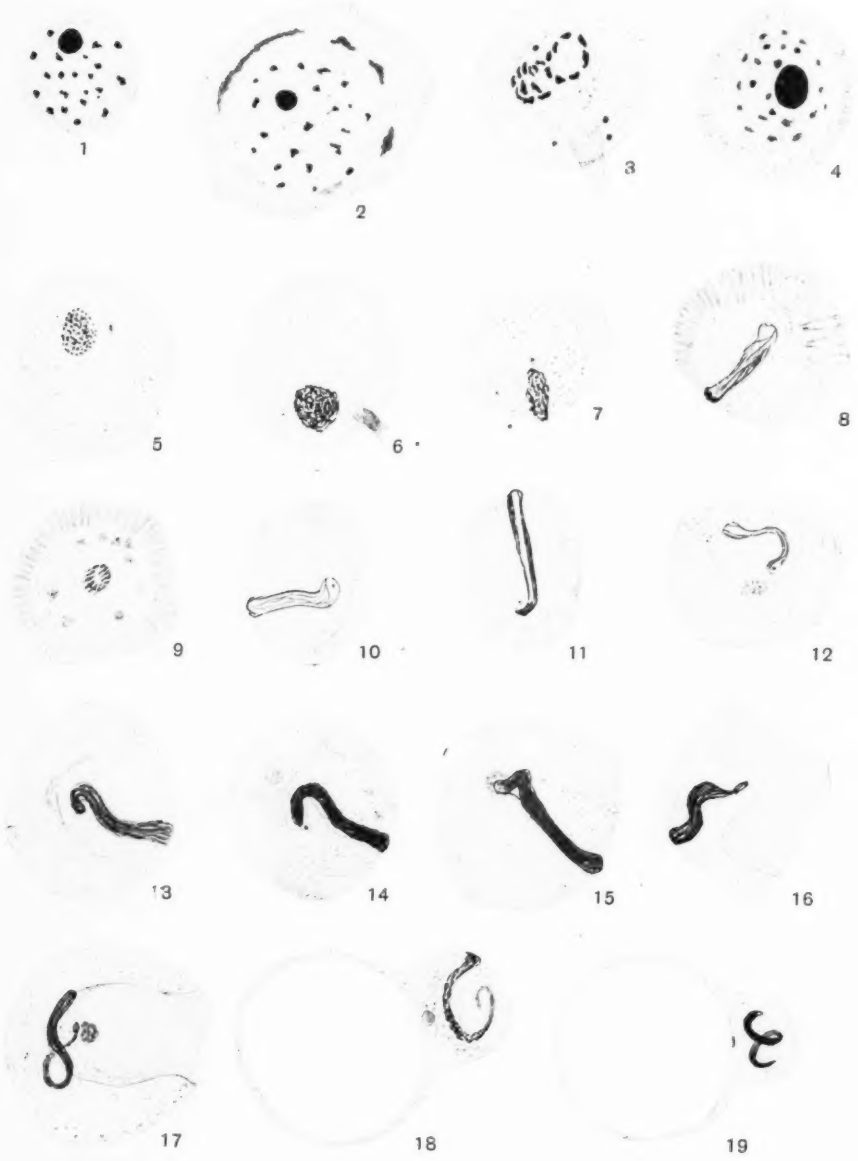
Fig. 25 *a*, *b*. Successive movements of the nucleus; the mitochondrial body has assumed a conical shape.

Fig. 26. Showing extension of nucleus along the plasma-rod; the central stainable cord of the latter is now visible.

Fig. 27. Showing transverse section of mitochondrial body in same phase as Fig. 22; part of the nucleus also appears in the section.

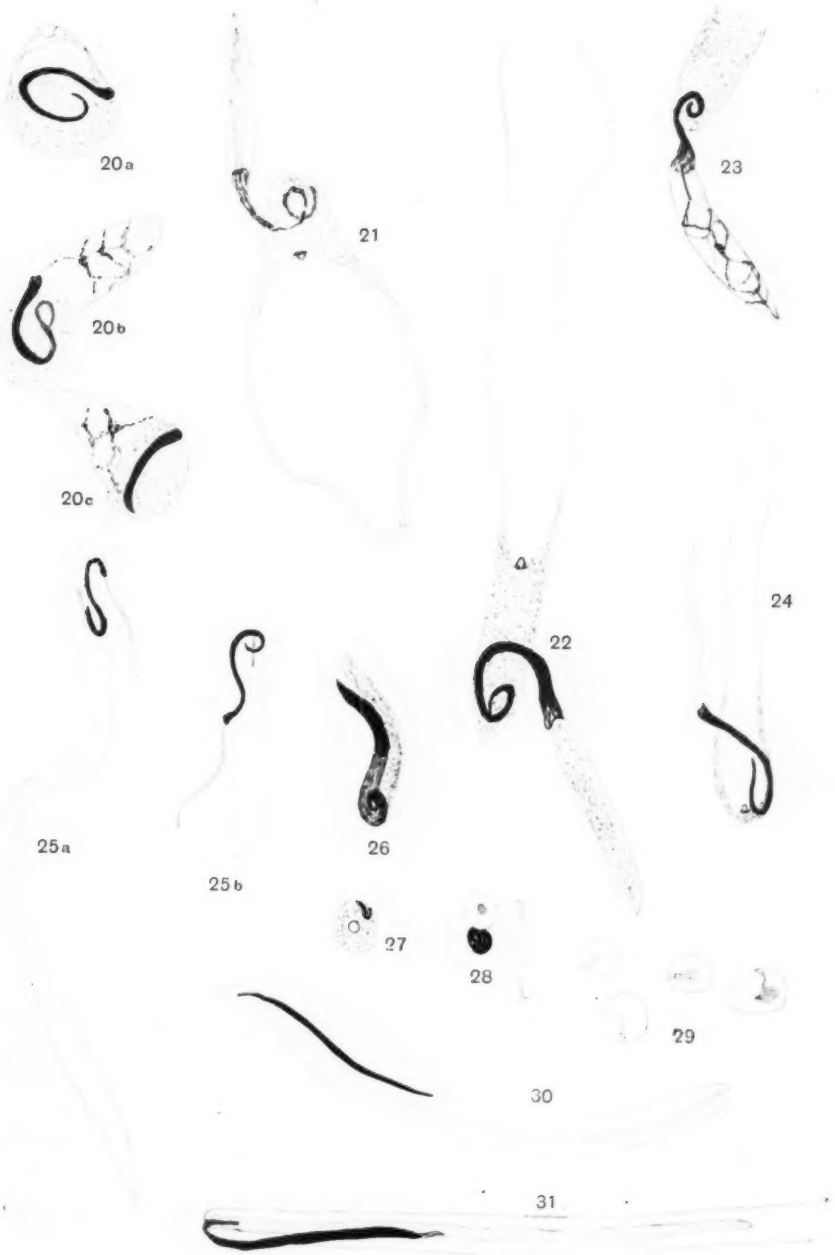
Figs. 28–29. Spermatozoa in transverse section, showing folding of central cord.

Figs. 30–31. Spermatozoa; final stage of development. Fig. 30 shows a spermatozoon from the vas deferens; Fig. 31 a somewhat younger stage with centrosomal corpuscle.



E. Nordenskiöld del.

PLATE XI



MALLOPHAGA FROM SOUTH AFRICAN BIRDS.

DESCRIPTIONS OF A NEW GENUS (*NEOMENOPON*) AND TWO NEW SPECIES (*MACHAERILAEMUS PLOCEI, NEOMENOPON PTEROCLURUS*).

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(With Plates XII and XIII.)

The species herein described both belong to the family Menoponidae. One of these species, collected by me from a Waxbill (a passerine bird) at Onderstepoort, Pretoria, belongs to the genus *Machaerilaemus* Harrison, the other, taken from a Sandgrouse in the Rustenburg District, Transvaal, by Mr Powell, together with specimens of a species of *Degeeriella*, I am placing in a new genus, for which I propose the name *Neomenopon*. These two new species are extremely interesting, in that they both possess a chitinous framework extending backwards from the anterior margin of the head for the support of the mandibles, a structure previously only known to occur in the genus *Eomenopon* Harrison, which was established partly on account of this structure. A similar structure, however, also occurs in a small unidentified species of *Menopon* taken from a Little Banded Goshawk (*Astur polyzonoides*) at Onderstepoort. This species may eventually prove to be sufficiently distinct in other details from the type of *Menopon* to warrant the founding of a new genus for its reception.

Curiously enough, both *Eomenopon* and *Machaerilaemus* were described by Harrison in the same paper in 1915, *Eomenopon* being established for the reception of a species found on two species of Australian Lorikeets, and *Machaerilaemus* being established for a species found on an Australian Grassfinch (a passerine bird). Since then Harrison has included Carriker's *Menopon laticorpus*, described from specimens found on an Ant-bird (*Thamnophilus doliatus*), a passerine bird, in Costa Rica, in the genus *Machaerilaemus*.

Machaerilaemus latifrons possesses a dark transverse band on the forehead, which is also present in both the species described here, and likewise in the *Menopon* from a hawk, but in these the bands are inconspicuous, very short, and are interrupted in the middle.

In the type of *Machaerilaemus* the mesothorax is separated from the metathorax, whereas in the new species described here these parts are fused together.

The following table will serve to differentiate the three genera: *Eomenopon*, *Machaerilaemus* and *Neomenopon*:

(1) Head not twice as wide as long, with a deep narrow cleft in the side of the forehead, extending to the inner border of the antennary fossa; chitinous framework for support of the mandibles present, extending backwards from the anterior margin of the head to form a pair of short free projecting spinous processes; meso- and metathorax distinct. *Eomenopon.*

Head more than twice as broad as long, without a cleft in the sides of the forehead; no spinous processes attached to the chitinous framework when present.

(2) Head with a large chitinous plate on the throat, flanked by two dagger-like processes (present or absent in *M. laticorpus*?) with or without a central circular perforation; chitinous framework absent or present; meso- and metathorax distinct or fused. *Machaerilaemus.*

No chitinous plate on throat; chitinous framework present; mesothorax fused with the metathorax. *Neomenopon.*

Genus Machaerilaemus Harrison.

Harrison (1915). *Parasitology*, VII. 389.

Machaerilaemus plocei, n. sp. (Plate XII, figs. 1–3).

Female. Ground colour pale brown, with darker markings of the same colour.

Head slightly more than twice as broad as long across temples. Forehead flatly rounded in front, abruptly rounded and swollen at the sides, with six hairs on each side. Eye with two minute hairs. Temples rounded, with four long hairs and several shorter ones. Occiput slightly concave, with two median hairs just inside the margin, and two more on each side, of which the outer one is the shorter. The only other hairs present on the dorsal surface are: two hairs on the forehead situated midway between the lateral angles and the middle line, the outer one being slightly longer than the inner one, and a short hair a little distance above these.

On the ventral surface the most conspicuous features are the chitinous framework, which has already been described; the gular plate and a more or less triangular plate on either side of this. The gular plate is heart-shaped, with a free projecting spinous process and five or six hairs on each side. Antennae with the two terminal segments indistinct. Palpi with the apical

segment the longest, the second and third sub-equal, and slightly longer than the first. Above the gular plate there are two hairs, and two more, slightly shorter, occur above these.

Thorax. The prothorax is winged, with two short spines, a long hair, and another short spine on each side, and a row of eight hairs on the posterior margin. The scapulars and interscapular bar are less developed than is usual in this family. On the prosternum there is a plate, and beneath this another plate, which extends on to the metasternum, the shape of these being shown in Pl. XII, Fig. 2. The metathorax has a row of about ten hairs on the posterior margin, and a long hair and several short spines at the postero-lateral angles. On the ventral surface, between the mid and hind coxae there is an inconspicuous plate clothed with shortish hairs.

Legs. The coxae are elongated; the second and third pairs each with five short spines, two being situated near the apex and three at the apex. Hind femora without a tuft of hairs or spines on the ventral surface. Mid and hind tibiae with several short spines near the apex.

The *abdomen* is elongate-oval, being broadest at the fourth segment. The tergites each with a pale brown transverse band, and a series of hairs on the posterior margin. On each sternite there is a dark transverse band, with three irregular rows of hairs on it, and with three or four short spines at the postero-lateral margins of the bands. The transverse band on the first sternite narrows out to a point at either end, and the bands on sternites six and seven are fused together. On the eighth sternite there is a narrow longitudinal blotch on either side of the median line, which broadens out posteriorly. The borders of the vulva are closely beset with a row of fine hairs.

The *pleurites* are dark brown, with several short hairs in the middle, and a row of longer ones and one or two spines on their posterior margins.

Male. The male resembles the female, except for the markings on the venter of the terminal segments, as will be seen by comparing Pl. XII, figs. 1 and 3, the former of which shows the ventral markings on the terminal abdominal segments.

The general form of the genitalia can be seen in Fig. 1.

Measurements in millimetres.

	Female		Male	
	Length	Breadth	Length	Breadth
Head	0·26	0·6	0·23	0·51
Prothorax	0·13	0·44	0·1	0·35
Metathorax	0·15	0·56	0·11	0·41
Abdomen	1·09	0·86	0·7	0·56
Total	1·63		1·14	

Described from one ♀ and one ♂ taken from a Waxbill at Onderstepoort, Pretoria, on 14. XII. 1918.

Genus NEOMENOPON, n. gen.

The genus may be characterised as follows: Head with distinct and fairly deep ocular emarginations; very broad, more than twice as wide as long; temples large. Prothorax with lateral margins rounded. Mesothorax fused with the metathorax. Pleurites well developed.

Neomenopon pteroclurus, n. sp. (Plate XIII, figs. 1, 2).

Female. Specimens preserved in alcohol are extremely dark, almost black, and it is then impossible to make out the markings. When mounted in Canada balsam, however, they are brown in colour, with dark brown markings. The *head* is extremely broad, being slightly more than twice as wide across the temples as long. The forehead is flatly rounded in front, and turns abruptly inwards on each side, extending backwards from the lateral angles in an almost straight line to the temples. On the margin of the forehead there are sixteen hairs, and on the dorsal surface there are six, situated in a line between the lateral angles; of these, one is situated on each side, midway between the median line and the lateral angle, and two—a long and a minute one—on each side between this hair and the margin. The temples are abruptly rounded, with about 10 long and short hairs on the margins. Occiput very slightly concave, with six hairs. Eye large, without a hair. On the ventral surface there is a chitinous structure for support of the mandibles, which consists of a band projecting backwards and slightly inwards on each side from the anterior margin to a short distance beyond the antennary fossa, where each is joined together by a transverse band. From each of the two angles formed by these bands there extends a curved band to the occipital margin. Above the transverse band there are two hairs, and above these are two shorter ones. The apical segment of the palpi is the longest, the third is the shortest, and the first and second sub-equal.

The shape of the two terminal segments of the antennae cannot be made out, owing to their being partly hidden by the pockets formed by the forehead and temples, which are very dark. On each side of the gular region there are four or five hairs in a longitudinal row.

Thorax. The prothorax is winged, with a short spine on each side in front, a long hair beneath it, and another short spine beneath this again; and on the posterior margin there are eight hairs. The interscapular bar does not quite reach the scapulars, and it is crossed by a median longitudinal bar.

The metathorax is shorter than the prothorax, with twelve hairs on the posterior margin, and a short spine on each side near the latero-posterior angles. On the metasternum there is a narrow longitudinal median plate bearing about ten hairs, and below this, between the mid and hind coxae, a median patch of nine hairs.

Legs. The coxae of the forelegs are elongated; coxae of mid and hind legs with three or four spines on or near their apical margins. The femora are very broad, and the hind pair each have a tuft of about 60 short hairs on their ventral surface.

The *abdomen* is broadly oval, being widest at the fourth segment. The tergites each have a pale transverse band (serrated on its posterior border) extending to, or almost to, the pleurites and with a series of about 18 to 20 hairs on their posterior margin. On each sternite there is also a transverse band, which is darker and not so wide as that on the corresponding tergite; on each band there is an irregular series of short hairs, which on tergites 3 to 6 form a more or less dense patch on the sides. The band on the seventh sternite is interrupted in the middle, the median space being filled by a still darker blotch, and the same appears to be the case on the sixth sternite, at least the median area is also darker than the rest of the segment. On sternites 7 and 8 there is a longitudinal blotch on each side of the median line, extending from the middle of the seventh to the apex of the eighth. The vulva is broadly rounded, with a series of fine short hairs on its margin.

The *pleurites* are well developed, brown in colour, with several hairs in the middle, and a series of longer ones and one or two small spines on their posterior margin.

Measurements in millimetres.

Female	Length	Breadth
Head	0·41	0·86
Prothorax	0·16	0·61
Metathorax	0·15	0·81
Abdomen	1·51	1·45
Total	2·23	

Described from one adult and two immature ♀♀ found on three specimens of Namaqua Sandgrouse (*Pteroclurus namaqua*) in the Rustenburg District, Transvaal, by Mr Powell in 1917.

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EXPLANATION OF PLATES XII AND XIII.

PLATE XII.

Machaerilaemus plocei, n. sp.

Fig. 1. Male, dorsal aspect.
Fig. 2. Male, head and prothorax, ventral aspect.
Fig. 3. Female, posterior abdominal segments, ventral aspect.

PLATE XIII.

Neomenopon pteroclurus, n. sp.

Fig. 1. Female, dorsal aspect.
Fig. 2. Female, head and prothorax, ventral aspect.

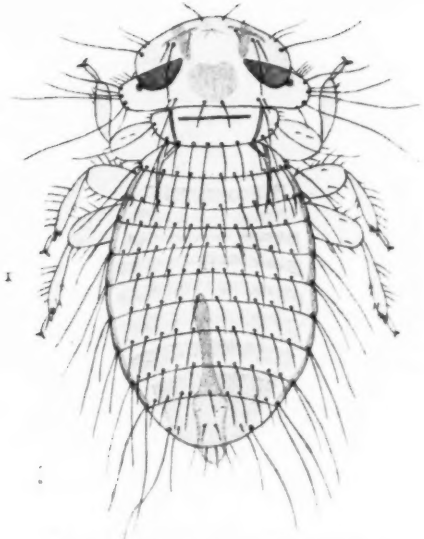

Fig. 1. *Machaerilaemus plocei*, n. sp. ♂

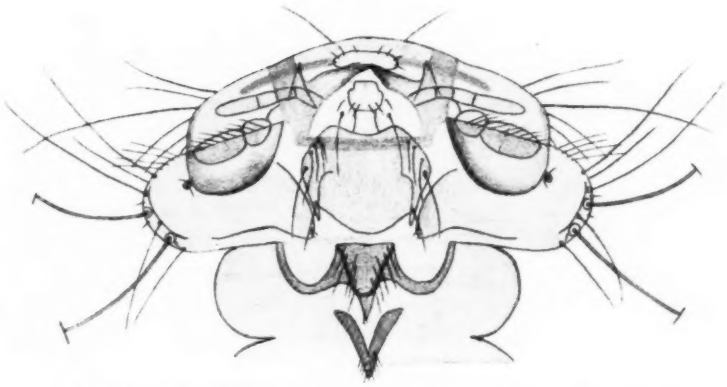

Fig. 2. *Machaerilaemus plocei*, ventral surface of head and prothorax of ♂

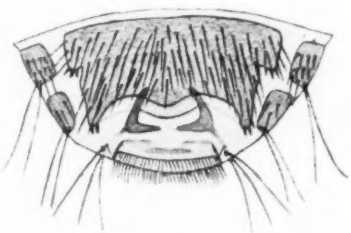

Fig. 3. *Machaerilaemus plocei*, ventral surface of terminal abdominal segments of ♀

G. A. H. B. del.

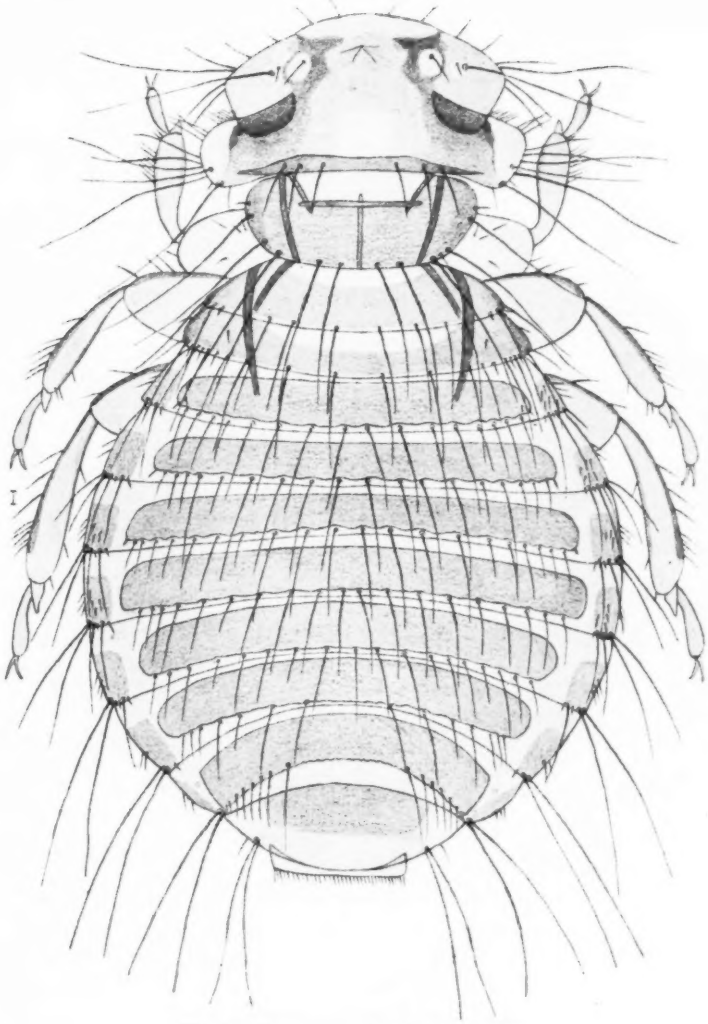

Fig. 1. *Neomenopon pteroclurus*, n. sp. ♀

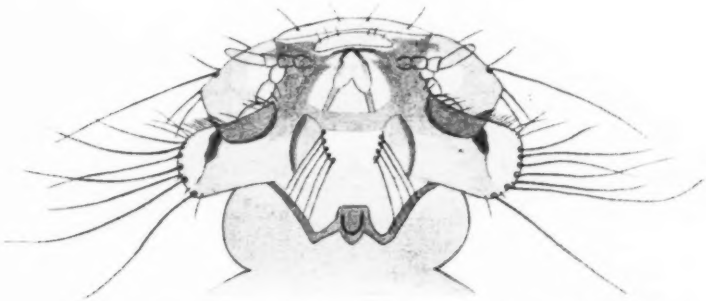

Fig. 2. *Neomenopon pteroclurus*, ventral surface of head and prothorax

G. A. H. B. del.

BODY-LICE UNDER SUMMER CONDITIONS IN MESOPOTAMIA.

By P. A. BUXTON, M.A., M.R.C.S.

(*Fellow of Trinity College, Cambridge.*)

During the summer months in Mesopotamia body-lice become extremely scarce on man, so much so that it may be difficult to find them even on men who are renowned for lousiness at other seasons of the year. When the nights become cold, as they often do rather suddenly towards the end of November, lice rapidly become numerous, this coinciding with the reissue of winter under-linen which has been stored through the summer in Ordnance dumps.

During my service as Entomologist to the Mesopotamian Force I constantly encountered officers, specialists in sanitation among them, who erroneously supposed that the lice survived the unfavourable conditions in summer as eggs in the stored warm clothing, the Ordnance being in fact blamed for distributing verminous clothing to various highly respectable units who would otherwise, as I was assured, not have suffered from these pests. I always pointed out that this was impossible in view of what we know of the duration of the egg and other stages of this insect, but as superstitions die hard it may be as well to record that during the summer of 1919, in the Persian plateau, which enjoys a summer as dry as that of Mesopotamia and only a little cooler, I could always find body-lice on 5 per cent. or 10 per cent. of Indian troops, even in one excellent unit the men of which were inspected by their own officers every week. In these dry hot summers lice appear to survive with difficulty and to breed very slightly. On the men in question I rarely found more than one or at the most two lice and this explains why their own officers failed to find them.

The Mesopotamian summer, which appears so unfavourable to reproduction, is generally very dry. Maximum shade temperatures pass 120° F. once or twice every summer, and pass 105° F. most days in the four summer months. Under active service conditions men were habitually exposed to higher temperatures than these official ones. In N.W. Persia, at Qazvin,

the official reading rarely exceeded 100° F. but ran up in tents to 115° F. most days for about two months. The climate was extremely dry.

This note may appear to entomologists to repeat what is known[1], but I publish it in the hope that it may perhaps help to convince that "practical man" the sanitarian.

[1] Consult Nuttall (*Parasitology*, x, pp. 87–91, 132; xi. pp. 205, 206) on seasonal variation in the number of lice on man.